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DYSFUNCTIONAL CHARACTERISTICS OF SMALL TROUT POPULATIONS

Final Research Report for
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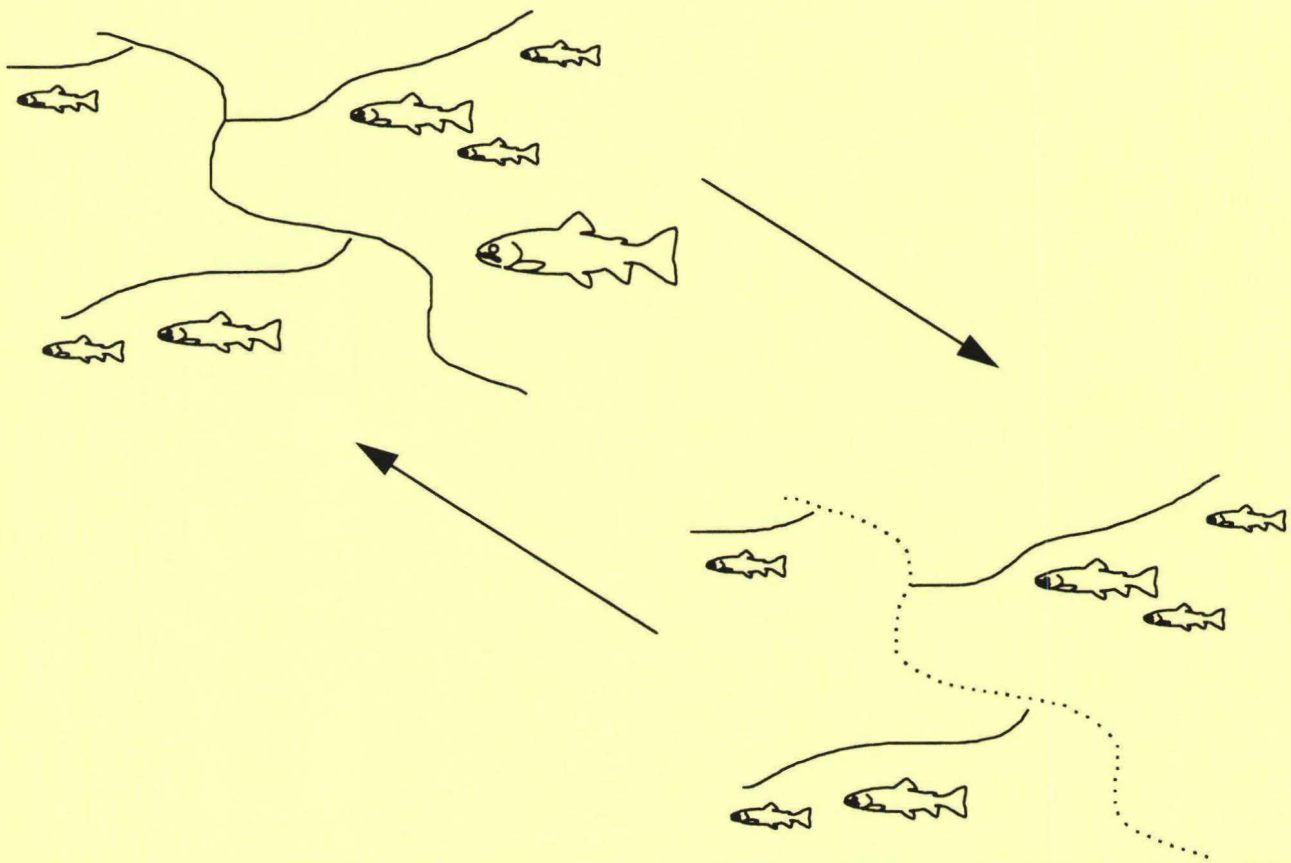

SUMMARY AND GENERAL INTRODUCTION

This report summarizes research on Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) conducted from 1992-1996 with funding from a Research Joint Venture Agreement (RJVA) with the USDA Intermountain Research Station (INT-92731-RJVA). The report is divided into four chapters, each submitted or soon to be submitted to peer-reviewed journals for publication. As a result, each chapter is 'self-contained' and has a slightly different format. Each chapter may be read separately, though many common themes run throughout the report. Our intention is to publish the four chapters of this report as separate papers to make the information more available to the general public. At the writing of this report, one chapter (Chapter 3) has been accepted for publication in the Canadian Journal of Fisheries and Aquatic Sciences, and a second (Chapter 4) is in revision for publication in Transactions of the American Fisheries Society. Chapter 1 is in review for publication in Environmental Biology of Fishes, and Chapter 2 is being prepared for submission to Conservation Biology. We view this as an important obligation, since Lahontan cutthroat trout are listed as threatened by the US Fish and Wildlife Service, and, with notable exceptions cited in the chapters, there is very little published information readily available in the peer-reviewed literature.

The original purpose of the RJVA was to study "dysfunctional characteristics of small trout populations," as indicated by the title of this report. Chapters 1 and 2 are specifically oriented

toward this objective. In Chapter 1, we reported results of three years of observational and comparative study of Lahontan cutthroat trout populations in relation to fragmentation of stream habitats. Fragmentation refers to the breakup of formerly continuous habitats. In stream habitats occupied by Lahontan cutthroat trout, fragmentation has reduced the average size of habitats and effectively isolated populations. Empirical and theoretical studies of trout and other species frequently point to habitat fragmentation as a significant threat.

In Chapter 1, data on fish occurrence, fish density, population size structure, individual movements and fish-habitat relationships are used to compare Lahontan cutthroat trout populations in fragmented and interconnected stream systems. We found that 1) local extinctions were widespread; 2) population structure and dynamics were complex, even within individual basins; 3) populations strongly responded to environmental variation among streams and years, and not to within-stream variation; and 4) fish adopted migratory lifestyles in large, interconnected drainages, but were more sedentary in small, isolated habitats. From these observations, we suggested habitat fragmentation increases the probability of local extinction in local populations of Lahontan cutthroat trout. In essence, we suggested that among-population processes (e.g. migration, dispersal, extinction and recolonization) may be more important that within-population processes (e.g. habitat size and small-scale environmental variation).

Our studies of Lahontan cutthroat trout in Chapter 1 indicated a large scale perspective was needed to more fully understand the factors associated with local extinctions. We reported results of a large-scale analysis of such factors in Chapter 2. We analyzed data from extensive presence-absence surveys for Lahontan cutthroat trout conducted by Nevada Division of Wildlife with multiple logistic regression to analyze the binary response (cutthroat presence or absence) in relation to habitat fragmentation, catchment basin size and shape, presence or absence of exotic salmonids, elevation and precipitation regime.

Results of this analysis in Chapter 2 were used to identify potentially important factors associated with local extinctions. We found that a single factor, whether or not a population was isolated (due to habitat fragmentation), was highly correlated with the occurrence of Lahontan cutthroat trout. None of the other variables in the study were significant in this regard. Results of this study supported and strengthened our conclusions in Chapter 1 and highlight the impacts of fragmentation of stream habitats on Lahontan cutthroat trout.

Chapters 3 and 4 of this report addressed more general questions in fisheries with Lahontan cutthroat trout data. In Chapter 3, we examined relationships between body size and population density of Lahontan cutthroat trout in an attempt to discover the relative important of biotic and physical factors on population size structure and dynamics. We also analyzed data

from other studies of trout in the Intermountain region to compare results among species. Results of our analyses motivated us to question the applicability of new theories that predict certain relationships between body size and population density in stream fishes and added insight into possible biotic and physical factors that may affect Lahontan cutthroat trout populations.

In Chapter 4, we discussed methods for analyzing fish-habitat relationships, with a special emphasis on within versus among-stream habitat variation. We showed that relationships between habitat variation at different spatial scales can be very complex, which has important implications for the design and statistical analysis of fish habitat surveys. Such surveys are very commonly conducted by resource agencies, and the results from our work should help to improve fish habitat surveys in the future. Data used in the analyses reported herein are given in Appendices 1-3, for those who like to see numbers.

Our work with Lahontan cutthroat trout, funded by the USDA Intermountain Research Station, has provided an important baseline for future study. With new funding from the US Fish and Wildlife Service, we will be able to collect at least three to four more years of data on Lahontan cutthroat trout. The data from this work will provide important new insights into the ecology and natural history of this and other fishes in the Great Basin, which should greatly benefit the management and recovery of Lahontan cutthroat trout.

CONTENTS

CHAPTER 1.....PAGE 5

CHAPTER 2.....PAGE 57

CHAPTER 3.....PAGE 89

CHAPTER 4.....PAGE 120

APPENDIX 1.....PAGE 144

APPENDIX 2.....PAGE 164

APPENDIX 3.....PAGE 167

Chapter 1.

Structure, dynamics and persistence of trout populations in relation to fragmentation of stream habitats

Synopsis

The structure, dynamics and persistence of stream-living Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) populations in the north-central Great Basin U.S.A. were studied over a three-year period to investigate the ecological effects of stream habitat fragmentation. Surveys of cutthroat occurrence in tweleve streams in fragmented and interconnected drainage basins indicated local extinctions are widespread and may not depend on population or habitat size. Population structure and dynamics were intensively studied in four isolated populations and three interconnected habitats. We observed widespread movement of individuals among interconnected habitats and relatively sedentary behavior in isolated habitats. In spite of this, we found little evidence to indicate that fish movement contributed to similarity in size structure or correlated population fluctuations among interconnected habitats. Highly correlated population fluctuations instead were attributed to similar environmental conditions. Similarly, population structure varied considerably across years and appeared to be related to elevational gradients in stream discharge and temperature. Variation in fish biomass was studied in relation to small-scale environmental variation (i.e. habitat variability within streams) and large-scale habitat variation (i.e. variation among streams). A significant interaction between stream-level habitat variation and annual variability in biomass was found, with little

relationship between fish biomass and small-scale environmental variation. Results of this study strongly suggest that Lahontan cutthroat trout populations are controlled by large-scale environmental variation that has strong spatial and temporal components. The diversity of habitats found within large interconnected drainage basins is essential to ensure long-term regional persistence of populations. Simplification of habitats by fragmentation and isolation of stream populations has dramatically increased the risk of regional extinction. Future efforts to recover this imperiled species must focus on large-scale restoration of spatially diverse and interconnected stream habitats to reverse the serious threat posed by habitat fragmentation.

Introduction

Declines of native fishes in North America have been attributed to loss of habitat, introduction and establishment of exotic species, pollution, and overharvest (Miller et al. 1989). These four threats have reduced the total amount of occupied habitat, and in many cases, formerly connected aquatic habitats are now isolated (Moyle and Leidy 1993). Such fragmentation of habitat is especially noticeable in stream-living salmonids, where water diversions and dams (Nehlsen et al. 1991), thermal barriers (Meisner 1990, Keleher and Rahel 1996) and downstream populations of exotic salmonids (Fausch 1989, Flebbe 1994) commonly act to displace native species to isolated headwater streams. Aquatic organisms restricted to headwater areas are expected to be most severely affected by stream habitat fragmentation (Zwick 1991). Because native salmonids are among the most imperiled of North American fishes (Miller et al. 1989) and typically occupy high-risk (extinction-prone) headwater stream habitats, there is a great need to understand the effects of habitat fragmentation on their population structure, dynamics and persistence (Rieman and McIntyre 1993, 1995a).

In this paper, we present results of a three-year investigation on the ecological effects of stream habitat fragmentation on Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) populations in headwater tributaries of the upper Humboldt River, Nevada. We classifed ecological effects of habitat fragmentation into processes that operate within and

among habitats. Within-habitat effects include edge effects (Harris 1984), reduced overall habitat area and total population size (Fahrig and Merriam 1993), and loss of habitat and life history diversity (den Boer 1968). Among-habitat processes that may be affected by habitat fragmentation include migration, dispersal and extinction-recolonization dynamics (Pulliam 1988, Gilpin and Hanski 1991, Harrison 1994). Within- and among-habitat processes may act synergistically to increase extinction risk of species in fragmented landscapes (Gilpin and Soulé 1987).

We studied ecological characteristics of Lahontan cutthroat trout populations in isolated and interconnected stream habitats to address the following questions about the effects of habitat fragmentation.

1) Are local extinctions in cutthroat populations related to habitat and/or population size?
2) Does among-habitat connectivity allow recolonization following local extinctions?
3) Does among-habitat connectivity and fish movement lead to correlated population structure and dynamics?
4) How do environmental factors influence cutthroat populations, and at what spatial scale?
5) What are movement patterns of cutthroat in connected and isolated stream habitats?

6) With regard to the above, what are the relevant spatial and temporal scales for understanding the effects of habitat fragmentation on Lahontan cutthroat trout?

To answer these questions, we studied; (1) the occurrence of Lahontan cutthroat trout in tweleve streams in fragmented and connected drainage systems; (2) population size structure and density in relation to habitat fragmentation; (3) correlations between fish biomass and site- and stream-level habitat variation; and (4) individual movements in isolated and connected streams. Lahontan cutthroat trout are classified as Threatened under the U.S. Endangered Species Act (Coffin and Cowan 1995). Results from this study will be useful in recovery efforts for this species. This study also will provide insight into the ecological effects of habitat fragmentation on stream fishes in general.

Study system

The study site is located in the upper Humboldt River drainage in the north-central Great Basin of Nevada (Fig. 1). Stream habitat conditions in this region are described by Nelson et al. (1987), Platts and Nelson (1988), Sada (1990) and Nelson et al. (1992).

Streams in this area harbored widespread populations of Lahontan cutthroat trout prior to the arrival of European

settlers approximately 150 years ago (Trotter 1987, Gerstung 1988). Since that time, cutthroat have become extirpated from approximately 90% of their original fluvial distribution (Coffin and Cowan 1995). Most remaining populations are isolated in small tributaries of formerly large, interconnected drainage networks (Coffin and Cowan 1995). Loss of mainstem river habitat is the primary reason for isolation of cutthroat in small tributary streams.

Habitat and population losses have been attributed to excessive disturbances associated with road construction, mine development, livestock grazing, water diversions for agricultural, mining and municipal purposes, and displacement by and hybridization with exotic salmonids (Trotter 1987, Gerstung 1988, Coffin and Cowan 1995). In the few basins where mainstem habitats still are suitable for cutthroat, populations in small tributaries are at least seasonally interconnected.

Generally, stream habitats are highly variable in space and time. Within years, however, seasonal fluctuations in stream discharge are fairly predictable. With the exception of episodic flooding from summer thunderstorms, peak discharges generally coincide with spring snowmelt and runoff in March-June. Variation in the timing and magnitude of spring runoff may have important impacts on fish community structure (Seegrist and Gard 1972, Erman et al. 1988, Sada 1990, Strange et al. 1992). Among years, periodic drought conditions contrast with cooler, wetter periods to cause dramatic changes in stream habitats with regard

to the frequency and magnitude of stream discharges (Fig. 2), water temperature, and physical characteristics of stream channels.

Spatial variation in habitat conditions also is marked (Table 1). Lahontan cutthroat trout populations in this study occupied streams ranging in elevation from 1700 to 2300 m. High-elevation streams are cooler in the summer (<20°C), with abundant riparian canopy cover, pool-forming rocks, and large woody debris in the channel. Lower elevation streams typically flow through permeable alluvial deposits (Nelson et al. 1992), with degraded (downcut) channels, lower canopy cover and higher summer water temperatures (>20°C). Many lower elevation habitats become intermittent or dry up completely during summer droughts. Lack of winter snow cover at lower elevations leads to colder water temperatures and anchor ice formation, possibly causing high fish mortality in some years (Nelson et al. 1992). Other fishes, including Piute sculpin (*Cottus beldingi*), speckled dace (*Rhinichthys osculus*), and Tahoe sucker (*Catostomus tahoensis*) were present in the study streams, but Lahontan cutthroat trout was generally the numerically dominant species. In one of our study streams (North Fork Humboldt River) Lahontan cutthroat trout coexist with numerically dominant introduced brook trout (*Salvelinus fontinalis*).

Methods

In this study we compared characterstics of populations in fragmented streams to those in contiguous or connected drainage systems (Fig. 1). Specific effects of fragmentation were studied by monitoring population persistence and recolonization, individual movements, and demographic and environmental correlations across habitats. Each is described below.

Population persistence and recolonization

Population persistence and recolonization were studied by monitoring cutthroat occurence in five isolated tributaries of the North Fork Humboldt River basin and seven connected tributaries in the Marys River basin (Fig. 1). Here, we use "tributary" as a synonym for "population." Although it can be argued that streams are continuous systems and such distinctions are artificial, the ecological distinctions between tributary and larger mainstem stream habitats (e.g. Minshall et al. 1983) justifies our choice. In the parlance of metapopulation dynamics (Gilpin and Hanksi 1991), we regard tributary streams as distinct habitat patches.

Cutthroat occurrence was monitored in 1993-4, primarily by sampling with a backpack electroshocker (Coffelt model BP-2). In 1993, visual surveys were conducted in streams with extremely low water volume and high water clarity. In one case (Hanks Creek),

our results are combined with those obtained by Nevada Department of Wildlife surveys (G. Johnson, Nevada Division of Wildlife, pers. comm.). Streams were surveyed by spot-electrofishing what we judged to be suitable habitat (e.g. relatively large pools with structural complexity, cf. Rieman and McIntyre 1995a). Other habitats (e.g. shallow pools, riffles and side channels) also were checked occasionally for the presence of young-of-year (age 0) fish. Visual surveys involved at least two observers who carefully looked for fish in streams as described for electrofisher surveys.

Stream populations were classified as "NE" (Nearly Extirpated, Table 2) when surveys in over 90% of the stream's length failed to locate more than two individuals. Because we cannot be absolutely sure fish were not missed in our surveys (cf. Reed, in press), we fully acknowledge the possibility of "false absences" due to our inability to exhaustively survey the entire length of each stream. This does not pose a major problem in our interpretation of cutthroat occurrence if it can be assumed that populations with fish densities low enough to be classified as NE are at very high risk of extinction. In general, populations experiencing such dramatic declines are assumed to be at high risk of extinction (Gilpin and Soulé 1987).

Population structure and density

Sampling methods. Population structure was studied intensively in three isolated (Frazer, Gance and Foreman Creeks) and three connected (Marys River Basin Creek and East and West Marys Rivers) streams in 1993-5 (Fig. 1). In 1994-5, an isolated tributary of the Marys River, "T" Creek also was surveyed (Fig. 1). To minimize differences due to within-season population changes, sampling was conducted over a 6-8 wk period during base flow conditions in summer and early fall (mid July to early October).

Fish populations were sampled using the multiple-pass depletion method as described by van Deventer and Platts (1989). All fishes were captured by electrofishing. Measurements taken on each fish included standard length (mm) and mass (to the nearest 0.1 g). Fish populations were sampled from 47 sites in six streams in 1993 and 49 sites in seven streams in 1994-5. Sample sites consisted of approximately 25 m sections of streams. Both up- and down-stream ends of each site were blocked with small-mesh seines (4 mm mesh diameter) to prevent fish escape during sampling. In each stream we sampled seven sites spaced 300 m apart over a 2 km stream length. Even spacing of sites ensured appropriate random selection of fluvial habitats in each stream. Three of the 49 sites established in 1993-4 had to be moved due to beaver pond formation during sampling in 1994-5.

New sites were established as close as possible to previous sampling locations.

Environmental correlations

Sampling methods. To study the effects of environmental variation on cutthroat abundance, a range of habitat variables were measured at the 49 sites sampled for fish abundance in 1994-5. Habitat features measured at each site and stream were among several found by Fausch et al. (1988) to be most strongly correlated with fish biomass in streams. Care also was taken to develop measures that have an acceptable degree of repeatability among recorders (Platts et al. 1983). Wetted channel width, average depth, maximum depth, instream macrophyte cover, and instream woody cover were measured on transects situated perpendicular to the stream channel and spaced two meters apart. Average depth across the channel was calculated from depth measurements taken at 25, 50, and 75% of the channel beginning from one bank (depth=0). At each point where depth was measured, the presence or absence of instream macrophyte or woody cover was scored. Canopy density was measured with a concave spherical densiometer (Lemmon 1956) every 4 m along each sample site following the method of Platts et al. (1987). Wetted channel width was determined as described in Platts et al. (1983). Large woody debris pieces, defined in this study as dead pieces of wood greater than 10 cm diameter and more than 3 m long (or solidly

embedded in the stream channel or bank), were counted at each site. Maximum dimensions (length, width, depth) of all undercut banks were measured at each site, and undercut volumes were calculated as half the volume of an ellipsoid. Conductivity (μS) and pH were measured with portable electronic meters.

Data analyses involved multiple linear regression using fish biomass ($g \cdot m^{-1}$) as the response, with 11 quantitative site-level variables and two qualitative variables ("stream" and "year") as predictors. Thus, all habitat data for 1994-5 were combined into a single predictive model of fish biomass. Site-level variables were screened with "all subsets" regression (Myers 1990). Multicollinearity, influence diagnostics, and potential nonlinearities were evaluated following recommendations in Freund et al. (1991) and Phillipi (1994). Variance heterogeneity was evaluated by Levene's test on the absolute residuals (Kuehl 1994). Log (base *e*) transformation of the response was used to stabilize variance heterogeneity. Following variable screening, we analyzed the reduced model as above, with qualitative stream and year effects included as "dummy" variables (Littell and Freund 1991).

Individual movements

Individual movements were monitored by examining recovery rates of marked individuals at population sampling sites in isolated streams and through an intensive capture-mark-recapture effort

throughout the Marys River basin (Table 3). We employed several marking techniques, including visible implant (VI) and PIT (passive integrated transponder) tags to identify larger individuals (>100 mm standard length) and fin clips or subcutaneously injected flourescent resin tags to identify batches of juvenile cutthroat (<100mm standard length).

Results

Population persistence and recolonization

Efforts to determine Lahontan cutthroat trout occurrence in seven tributaries of the Marys River and five in the North Fork Humboldt River basins during 1994-5 are summarized in Table 2. Near or complete extirpations of previously known populations were observed in three Marys River (Short, Chimney and Cutt Creeks) and two North Fork Humboldt River tributaries (Mahala and Jim Creeks) in 1993. In 1994, surveys in the Marys River revealed populations of age 1 cutthroat in Short and Chimney Creeks, but no cutthroat in Cutt Creek. In surveys of the North Fork Humboldt basin, cutthroat were still absent from Mahala Creek in 1994, but a small population of age 1 cutthroat was found in Jim Creek. In a follow-up survey on Jim Creek in 1995 we again found no cutthroat.

Population structure and density

Population structure was highly variable in space and time (Figs 4-6). In 1993, only Frazer and Gance Creeks had young-of-year cutthroat at the time surveys were conducted (indicated by the size class peaking at ~35 mm). Ripe male cutthroat were observed in mid-August in the West Marys River, and small (<20 mm) cutthroat fry were seen in Foreman Creek in early October. A very small number of small (<50mm) cutthroat were captured in Foreman Creek, but it is unclear if these fish were actually young-of-year fish, and in any case they represent only a very small fraction of the total population (see *Population structure and dynamics* in **Discussion**).

In 1994, size structure changed dramatically in all streams (Fig. 5). Young-of-year cutthroat appeared in East Marys River and Marys River Basin Creek due to earlier emergence. Young-of-year cutthroat were found in T Creek as well. Young-of-year cutthroat also were present again in Frazer and Gance Creeks, but in lower numbers than in 1993 (Figs 5, 7). As in 1993, no young-of-year cutthroat were captured in West Marys River and Foreman Creek, but small (<20 mm) cutthroat fry were observed in stream margins. Recruitment from the 1993 year class in both West Marys River and Foreman Creek, is indicated by the appearance of fish between 50 and 100 mm standard length (Fig. 5).

In 1995, young-of-year only were captured in Frazer and Gance Creeks (Fig. 6). One small (31 mm) cutthroat was captured

during sampling of Foreman Creek in 1995, but only one other similarly sized individual was observed outside the sample sites. The Foreman Creek population of age 1 and older fish was substantially smaller in 1995, indicating a loss of older, larger fish. Small cutthroat fry were observed in East Marys River in mid-August, but none were seen in Marys River Basin Creek, T Creek or West Marys River.

Plots of fish abundance through time (Fig. 7) indicate that population fluctuations were highly correlated among Marys River tributaries, while fluctuations among Frazer Creek and the North Fork tributaries (Foreman and Gance Creeks) were less similar (Table 4). In most cases, changes in population density were most strongly affected by the presence of young-of-year fish (Fig. 7). Note that Foreman Creek population densities were remarkably constant (Fig. 7) in spite of the changes in size structure that occurred in 1993-5 (Figs 4-6). Overall, changes in population size were marked, especially in Marys River Basin Creek and East Marys River (Fig. 7).

Environmental correlations

Multiple regression failed to reveal significant relationships between fish biomass and any of the 11 site-level habitat variables measured in 1994 or 1995. Average wetted width, instream macrophyte cover and woody cover, and pH were all significantly related to fish biomass ($P<0.05$, results not shown)

until stream and year effects were entered into the model. Qualitatitive stream and year effects were highly significant with a significant stream*year interaction (Table 5).

Individual movements

Of 199 fish marked in the Marys River system, only one individual was recaptured. It was marked originally in 1994 in the mainstem Marys River and travelled over 3 km upstream into the middle section of the East Marys River, where it was captured in 1995. Indirect evidence of movement came from surveys in 1995. In the mainstem Marys River, sites that dried completely in the 1994 drought were recolonized by cutthroat in 1995. Recapture attempts in sites where large numbers of fish were marked, including one site in Marys River Basin Creek, where 64 individuals were marked in 1994, failed to locate marked individuals. Finally, the upstream-most site in Marys River Basin Creek contained no cutthroat in 1993-4, but was colonized in 1995 in spite of its location above several waterfalls previously assumed to be migration barriers.

In contrast to the Marys River results, at least 30 percent of fish marked in isolated streams were recaptured in exactly the same site they were marked in previous years (Table 3). Exceptions were Gance Creek, where low numbers of adults were marked, and Foreman Creek, where loss of large adults (including marked fish) from study sites occurred in 1995. Searches were

not conducted outside of study sites, so the loss of marked individuals might have been due to in situ mortality, emigration, or a combination of both.

Discussion

Results of this study point to the importance of among-habitat processes in the structure, dynamics and persistence of Lahontan cutthroat trout populations. Our results suggest that 1) local extinctions are relatively widespread; 2) population structure and dynamics are complex, even within individual basins; 3) populations strongly respond to environmental variation among streams and years, and not within-stream variation; and 4) Lahontan cutthroat trout adopt migratory lifestyles in large, interconnected drainages, but become sedentary in small, isolated habitats. We discuss each of these points in relation to the problem of habitat fragmentation below.

Population persistence and recolonization

Results of extinction-recolonization studies provide interesting insights into the importance of these processes in highly stochastic environments such as those encountered by Lahontan cutthroat trout. The fact that cutthroat population sizes are highly variable is well documented in this and other studies (Platts and Nelson 1988). Our sample of extirpated or near-

extirpated populations is small (n=6), but results suggest that the highly variable nature of cutthroat habitats renders even relatively large populations vulnerable to extinction. Two specific examples will illustrate this point.

Jim Creek in the North Fork Humboldt River subbasin (Fig. 1) was sampled by electrofishing in 1993, but no cutthroat could be found (Table 3). A second electrofishing effort in 1994 revealed several concentrations of juvenile (age 1) cutthroat in a ~1-2 km reach. Cutthroat were absent from up- and down-stream areas, including relatively large, active beaver ponds. The nearest stream that could serve as a potential source of colonists is Mahala Creek (Fig. 1), which did not have cutthroat in either 1993 or 1994 (Table 2). The most likely explanation is the juveniles in 1994 were produced from a very limited number of spawning adults that survived in Jim Creek. Jim Creek provides an example of the potential for cutthroat to persist in small isolated habitats. This population may now be extirpated, however, following the severe drought of 1994 (JBD, pers. obs.).

In contrast to the persistent Jim Creek population is the decline of a formerly large cutthroat population in Hanks Creek in the lower Marys River basin (Fig. 1). Hanks Creek was known to harbor large (> 200 fish·km^{-1}) cutthroat populations in the past (Coffin 1983). Surveys in June of 1994 revealed only a single cutthroat (in poor condition) over more than 7 km sampled in lower Hanks Creek. Subsequent surveys by Nevada Division of

Wildlife in 1994 failed to find cutthroat in upstream areas (G. Johnson, pers. comm.).

Two tentative conclusions regarding extinction-recolonization can be reached by considering the cases described above. First, isolated streams that have lost their cutthroat populations cannot be recolonized. Such is the case with Mahala Creek in the North Fork Humboldt basin. In fragmented stream systems, extinctions will proceed in a ratchet-like manner and the chances of basin-wide extinction are increased. Second, the above case histories for cutthroat provide little evidence for a relationship between habitat *or* maximum population size and extinction risk. Other factors, such as the frequency and magnitude of physical and biological disturbance probably play a larger role in population persistence (discussed below).

The apparent lack of a relationship between habitat size and cutthroat occurrence is perhaps a surprising result. A recent large-scale analysis of presence and absence in another stream-living salmonid (bull trout, *Salvelinus confluentis*) found probability of occurrence to be significantly related to habitat size (Rieman and McIntyre 1995a). We have recently completed a similar large-scale analysis of Lahontan cutthroat trout that supports our finding here that habitat size and occurrence are not related, however (JBD, unpubl. data).

The mechanism by which recolonization occurs in interconnected tributary habitats is not clear. Recolonization of habitats may occur from resident individuals persisting in

small refugia within the stream itself or via spawning by adults from mainstem habitats, or perhaps a combination of both. In the interconnected Marys River basin, few of the fish captured in Short and Chimney Creeks in 1994 were large enough to be classified as adults (all were <125 mm standard length). The fact we did not capture any large adults in these streams, however, cannot be taken as evidence that these fish were the result of spawning by adults from the mainstem Marys River because they may have been missed during our surveys.

A final comment regarding our observations on population persistence concerns the distinction between apparent extirpation and juvenile emigration in the Marys River basin. Our failure to locate fish in Cutt, Short and Chimney Creeks in 1993 may be due to the fact that juvenile salmonids in small tributaries commonly emigrate to spend their adult lives in larger mainstem riverine habitats (Northcote 1978, 1992). Previous researchers (Nelson et al. 1987, R.L. Nelson, pers. comm.) have noted the presence of large adult fish in these streams, however. For this and reasons given below, we believe fish absence in these streams in 1993 was due to in situ mortality rather than emigration.

In 1994, we visited Chimney Creek twice during the summer, once in June and later in July. During the first visit in June, fish were located throughout the upper reaches of Chimney Creek, but later in July only a few isolated groups of fish remained. Several isolated pools that contained fish in June had dried, undoubtedly resulting in fish mortality. Furthermore, the lower

reaches of Chimney Creek had no surface flow, and thus emigration into the mainstem Marys River was impossible. From this, we surmise that stream desiccation during the drought conditions of 1994 was responsible for this loss of fish habitat and mortality in isolated pools. Such conditions prevailed in the years preceding this study when drought conditions persisted for several years (Fig. 2), very likely causing widespread extirpation of Lahontan cutthroat trout in many stream habitats. Factors that allow fish to survive under drought conditions, such as cold water refugia afforded by groundwater flow (Nielsen et al. 1994) may be critical in terms of population persistence and require further study to determine their importance.

Population structure and dynamics

If habitat fragmentation interrupts among-habitat movements, and fish are highly migratory (Gowan et al. 1994), then population structure should be more similar among connected streams and less similar among isolated streams. In other words, widespread movement of individuals among streams may counter the effect of differing environmental conditions on population structure. We found little evidence to support this in our study streams. Even though there is evidence for widespread movement of individuals within the Marys River basin (see *Fish movement* below), size structure data (Figs 4-6) indicated substantial temporal and spatial variation, even among interconnected populations

separated by only a few kilometers (e.g. West and East Marys Rivers).

Fluctuations in population density were, however, tightly coupled among interconnected habitats in the Marys River basin (Table 4, Fig. 7). We chose to represent population density in terms of fish·m^{-3}, but other measures of density, including fish·m^{-2} and fish.m^{-1} were highly correlated ($r > 0.90$) with this measure. Data from T Creek in the Marys River basin suggest correlated population fluctuation among interconnected habitats is a result of correlated environmental conditions rather than among-population movement of individuals (also see Rieman and McIntyre 1995b). T Creek is a tributary to the lower Marys River, but is effectively isolated by unsuitable habitat in its lower reaches. T Creek should have environmental conditions similar to those in tributaries to the upper Marys River (Fig. 1), however, because it drains a divide adjacent to Marys River Basin Creek. We have only two years of data, but the timing of fry emergence and changes in total population density in T Creek closely parallel that in the two adjacent drainages in the Marys River basin (Marys River Basin Creek and East Marys River, Fig. 7).

Based on the timing of fry emergence, we found three general stream types. Higher elevation streams, such as Foreman Creek and West Marys River almost never have young-of-year cutthroat populations until at least September. Fry emergence in higher elevation streams such as T Creek, East Marys River and Marys

River Basin Creek, occurs earlier, but young-of-year populations are present during the summer only in very warm years (e.g. 1994). Low elevation streams such as Frazer and Gance Creeks always have young-of-year by July. The appearance of small (~35 mm) individuals in Foreman Creek in 1993 and 1995 complicates our characterization of Lahontan cutthroat trout populations. The small fish in Foreman Creek may have been slow-growing juveniles or the product of a bimodal spawning chronology (Nelson et al. 1987). Attempts to age these individuals from scale samples were complicated by the fact that late-emerging trout often fail to form first-year annuli (Lentsch and Griffith 1987).

Recruitment timing is thought to play an important role in the response of salmonid populations to environmental stochasticity (Seegrist and Gard 1972, Erman et al. 1988, Strange et al. 1992). In large, elevationally diverse basins such as the Marys River, within-basin habitat heterogeneity may lead to asynchronous timing of recruitment (Fig. 7). Theoretical studies show such asynchrony in metapopulations decreases the chance of simultaneous extinctions at a regional scale (den Boer 1968, Quinn and Harrison 1989).

Environmental correlations

Many of the site-level habitat variables analysed in this study were among those found by Fausch et al. (1988) to be the best predictors of fish biomass in streams. Their influence on

cutthroat biomass, however, was minor in comparison to stream-level and year effects. The prevalence of stream and year effects may stem from the harsh and unpredictable conditions faced by Lahontan cutthroat trout populations. Stream discharge, for example, was highly variable during the course of this study. The most severe drought in 50 years occurred prior to this study (Fig. 2) and drought conditions in 1994 resulted in extensive stream desiccation and fish mortality in the Marys River (JBD, pers. obs.). Crowding caused by low water levels may have intensified intraspecific competition for food and/or space as well (Dunham and Vinyard, in press).

Stream and year effects observed in this study probably were due, at least in part, to the response of Lahontan cutthroat trout populations to stream discharge. The importance of stream-level influences on cutthroat populations is especially relevant in light of habitat fragmentation. As discussed above, the importance of correlated population fluctuations, environmental variability, and connectedness are central to the persistence of subdivided populations. From our analysis of fish habitat relationships, it is clear that large-scale spatial and temporal environmental variability play a central role in the dynamics of Lahontan cutthroat trout populations.

Individual movements

Several authors have noted that stream-living salmonids can be highly migratory and that this behavior may be adaptive (reviewed in Northcote 1978, Northcote 1992, Gowan et al. 1994). In some situations, however, migratory behavior actually may be selected against. Such is the case with isolated salmonid populations above waterfalls (Northcote and Hartman 1988, Northcote 1992), where the consequences of downstream migration are lethal. This also may be the case for Lahontan cutthroat trout in isolated tributary streams. Individuals that migrate too far downstream may experience degraded habitat conditions, unsuitable temperatures and stranding as streams dry in summer months. John (1964) described such a scenario for speckled dace (*Rhinichthys osculus*) in isolated stream habitats in Arizona.

Because exhaustive searches for marked individuals were not conducted in isolated streams, we have no direct evidence of individual movements. High numbers of recaptured individuals in sample sites in isolated streams contrast sharply with our lack of success in locating marked individuals in the interconnected Marys River basin, however, where marking and recapture efforts were much higher. High rates of individual movement in the Marys River basin also are suggested by recolonization of extensive areas of stream that dried completely in 1994, and by the ability of cutthroat to surmount substantial migration barriers (see also Diana et al. 1978). Finally, though only one marked fish was

recaptured in the Marys River basin, it had migrated over 3 km. We therefore hypothesize that isolation of Lahontan cutthroat trout in small tributary streams creates environmental conditions that favor sedentary behavior.

Conclusions

Results of this study only cover a very brief snapshot of time in terms of assessing the long-term (i.e. 10^2-10^3 generation) population viability of Lahontan cutthroat trout populations in relation to fragmentation of stream habitats. Only long-term research on populations can fully address such issues (Elliott 1994). By using a variety of methods to investigate the ecological effects of habitat fragmentation over a relatively large spatial scale, we hope to have captured a substantial portion of the natural variability that Lahontan cutthroat trout experience.

Habitat fragmentation may increase extinction risk in stream-living fishes by 1) reducing average population sizes in habitat fragments (Schoener and Spiller 1992, Rieman and McIntyre 1993), 2) causing loss of population 'rescue' by immigration and recolonization (Brown and Kodric-Brown 1978, Stacey and Taper 1992), 3) causing loss of habitat complexity (Pearsons et al. 1992), and 4) causing loss of life-history variation (Rieman and McIntyre 1993, Gresswell and Liss 1994). In short, habitat fragmentation simplifies stream habitats and reduces the

potential for spreading of risk among populations (den Boer 1968). Den Boer (1968) distinguished several types of risk spreading that may increase the overall persistence of populations, including spreading of risk by phenotypic variation, within-population variability in time and space, and in relation to other species. With the exception of the last point concerning species interactions, we found much evidence to support den Boer's idea of risk spreading among streams in the Marys River basin. Loss of complexity and connectivity in other basins, such as the North Fork Humboldt River may increase the long-term probability of basin-wide extinction.

These findings have implications for conservation of endangered salmonids and lead us to question the wisdom of the traditional emphasis on maximizing fish biomass by managing within-habitat features (cf. Reeves et al. 1991). In the case of Lahontan cutthroat trout, the emphasis should be placed on population *persistence* rather than *production*. Delisting criteria in the Lahontan cutthroat trout recovery plan call for populations with a 95% probability of persistence for 100 years (Coffin and Cowan 1995). Highly productive, but isolated populations are still vulnerable to extirpation by catastrophic disturbances such as droughts and extreme runoff events, and cannot be recolonized. Such populations are unlikely to meet the persistence criteria required for delisting of Lahontan cutthroat trout (Coffin and Cowan 1995). If long-term conservation of natural Lahontan cutthroat trout populations is to be realized,

limited resources may be more usefully diverted to restoration of diverse interconnected drainage networks. Managing within-habitat characterstics may locally enhance populations, but larger scale (and less controllable) environmental variation may render such efforts fruitless if regional population processes are ignored.

Acknowledgements

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Table 1. Physical characteristics of stream habitats in this study (Fig. 1). Values for elevation, depth and width are stream averages[1].

Locality	Basin (km^2)	Elevation (m)	Depth (cm)	Width (cm)
Frazer Creek	27	1975	13	156
N. Fork Humboldt River	116	2556	-	-
Foreman Creek	21	2544	11	242
Jim Creek	13	2195	-	-
Mahala Creek	14	2150	-	-
Gance Creek	33	2165	10	158
West Marys River	32	2670	16	315
East Marys River	13	2670	12	276
Marys River Basin Creek	19	2504	13	279
T Creek	26	2360	11	258
Short Creek	4	2180	-	-
Chimney Creek	17	2315	-	-
Cutt Creek	2	2415	-	-
Hanks Creek	114	2140	-	-

[1]Values for stream depth and width are from 1995.

Table 2. Summary of occurrence and relative abundance of Lahontan cutthroat trout in tweleve tributaries of the North Fork Humboldt and Marys River basins 1993-4.

Locality	Fish abundance[1]	
	1993	1994
North Fork Humboldt River Basin		
North Fork Humboldt River	Common	Common
Foreman Creek	Common	Common
Mahala Creek	NE	NE
Jim Creek	NE	Rare
Gance Creek	Common	Common
Marys River Basin		
West Marys River	Common	Common
East Marys River	Rare	Common
Marys River Basin Creek	Rare	Common
Short Creek	NE	Rare
Cutt Creek	NE	NE
Chimney Creek	NE	Common
Hanks Creek	Not surveyed	NE

[1]Abundance categories defined as follows: Common refers to populations with > 50 fish·km^{-1}; Rare refers to < 50 fish·km^{-1}; NE (Near Extirpation) refers to < 1 fish·km^{-1}.

Table 3. Numbers of fish marked (M) and recaptured (R) in all streams, 1993-1995. Asterisks indicate fish marked outside of sample sites. Numbers in parentheses indicate percent recaptured ($[R / M_{year-1}] \cdot 100$).

	1993		1994		1995	
Stream	M	R	M	R		
Frazer Creek	33	12	(36.4)	8	6	(30.0)
Gance Creek	6	0		3	0	
Foreman Creek	25	8	(32.0)	24	0	
MR Basin Creek	1,2*	0		64*	0	
East Marys River	2,1*	0		16*	1	(0.05)
West Marys River	4,9*	0		12,24*	0	
Upper Marys River	0	0		34*	0	
Lower Marys River	0	0		5*	0	
Chimney Creek	0	0		22*	0	
Short Creek	0	0		3*	0	

Table 4. Pearson correlation matrix of total population density (Fig. 7) for streams sampled 1993-5. Numbers in parentheses are *P*-values. Values in bold text highlight correlations among connected and isolated habitats (upper right and lower left corners of matrix).

	Connected habitats		Habitat fragments			
	East Marys River	MR Basin Creek	West Marys River	Frazer Creek	Foreman Creek	Gance Creek
EMR	1.00					
	-					
MRBC	**1.00**	1.00				
	(0.02)	-				
WMR	**1.00**	**1.00**	1.00			
	(0.02)	**(<0.01)**	-			
FC	0.29	0.31	0.31	1.00		
	(0.82)	(0.80)	(0.80)	-		
FN	0.64	0.66	0.66	**0.92**	1.00	
	(0.56)	(0.54)	(0.54)	**(0.26)**	-	
GC	0.98	0.98	0.98	**0.49**	**0.80**	1.00
	(0.14)	(0.12)	(0.12)	**(0.68)**	**(0.42)**	-

Table 5. Analysis of variance table for analysis of fish biomass (g fish · m^{-1}) in relation to stream, year and stream*year effects. Model R^2 = 0.86.

Source	df	MS	*F*	*P*
Year	1	81.07	250.08	0.0001
Stream	6	10.66	32.87	0.0001
Stream*year	6	2.00	6.17	0.0001

Figure Captions

Fig. 1. Map of the upper Humboldt River drainage basin, northeast Nevada, U.S.A., with arrows indicating streams mentioned in the text. Solid lines indicate approximate distribution of stream habitats supporting Lahontan cutthroat trout (see Gerstung 1988, Coffin and Cowan 1995).

Fig. 2. Average spring discharge in the lower Marys River from daily U.S. Geological Survey records, 1944-1995 (B. Bostic, Carson City, NV, pers. comm.).

Fig. 3. Size structure of Lahontan cutthroat trout populations sampled in 1993. See Fig. 1 and text for detail on localities. Numbers in parentheses are numbers of fish captured at all seven sites within each stream. Units on the horizontal axis are increments of 5 mm.

Fig. 4. Size structure of Lahontan cutthroat trout populations sampled in 1994. See Fig. 1 and text for detail on localities. Numbers in parentheses are numbers of fish captured at all seven sites within each stream. Units on the horizontal axis are increments of 5 mm.

Figure Captions (cont.)

Fig. 5. Size structure of Lahontan cutthroat trout populations sampled in 1995. See Fig. 1 and text for detail on localities. Numbers in parentheses are numbers of fish captured at all seven sites within each stream. Units on the horizontal axis are increments of 5 mm.

Fig. 6. Population density estimates for Lahontan cutthroat trout populations sampled 1993-5. Error bars are standard errors. Note the symbol for total density only occurs when more than one age class is present. "YOY" means young-of-year (age 0) fish.

Figure 1.

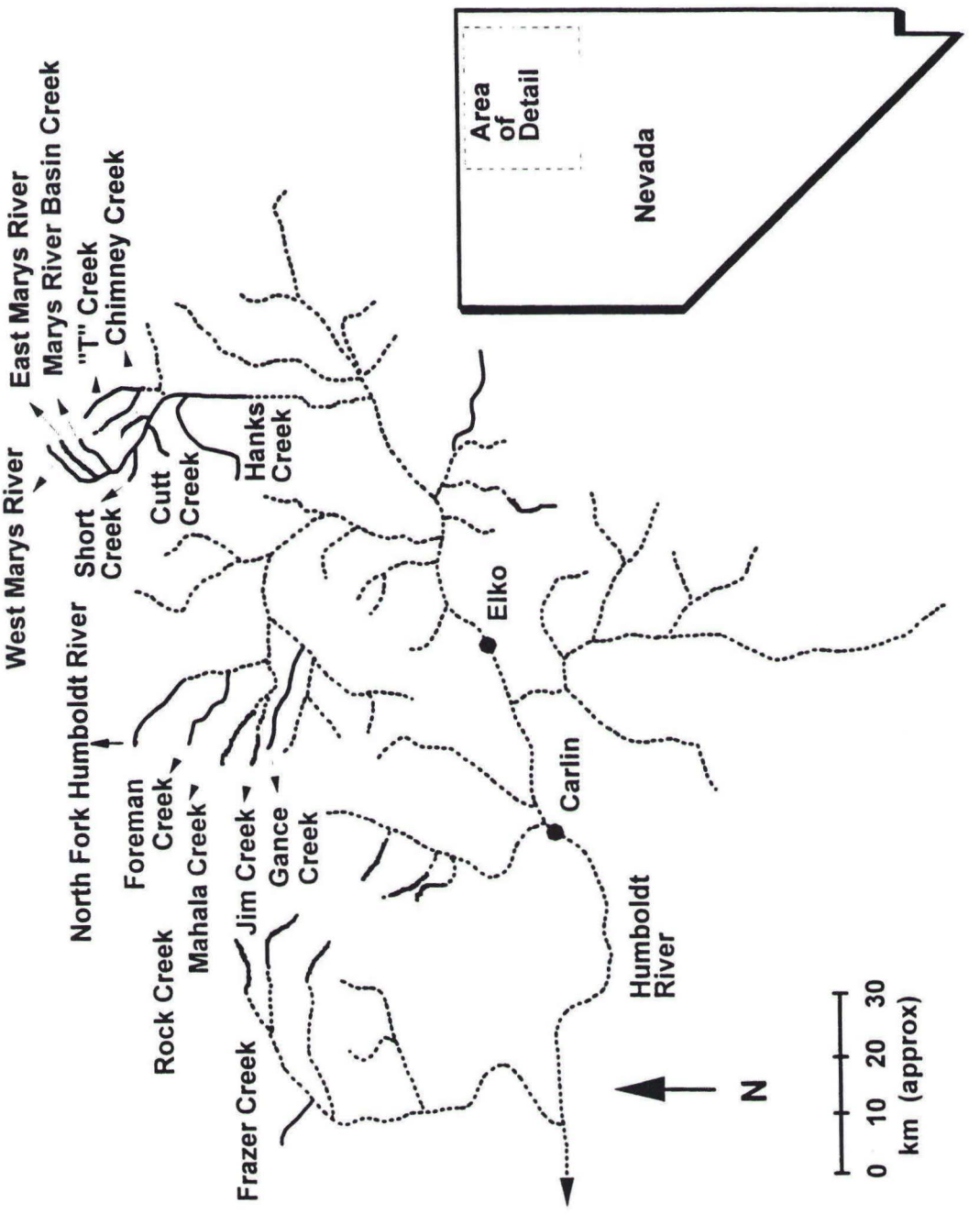

Area of Detail
Nevada
West Marys River
East Marys River
Marys River Basin Creek
"T" Creek
Chimney Creek
Short Creek
Cutt Creek
Hanks Creek
North Fork Humboldt River
Foreman Creek
Rock Creek
Mahala Creek
Jim Creek
Gance Creek
Frazer Creek
Elko
Carlin
Humboldt River
N
0 10 20 30
km (approx)

Figure 2.

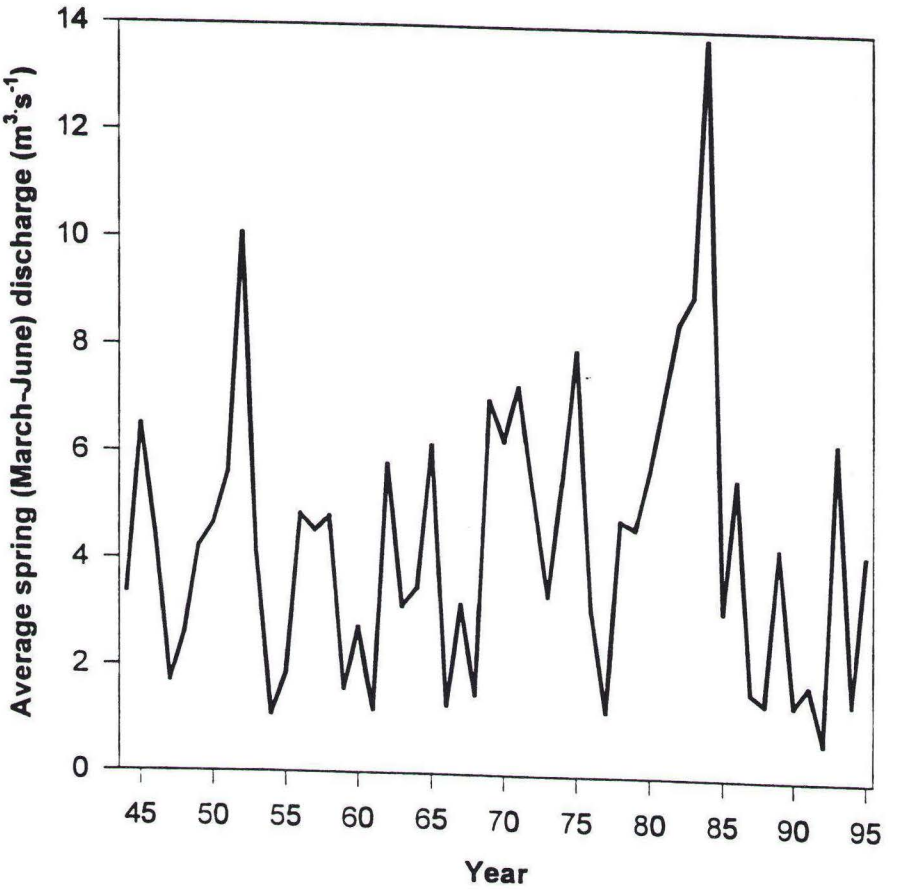

Average spring (March-June) discharge ($m^3 s^{-1}$)
0
2
4
6
8
10
12
14
45
50
55
60
65
70
75
80
85
90
95
Year

Figure 3.

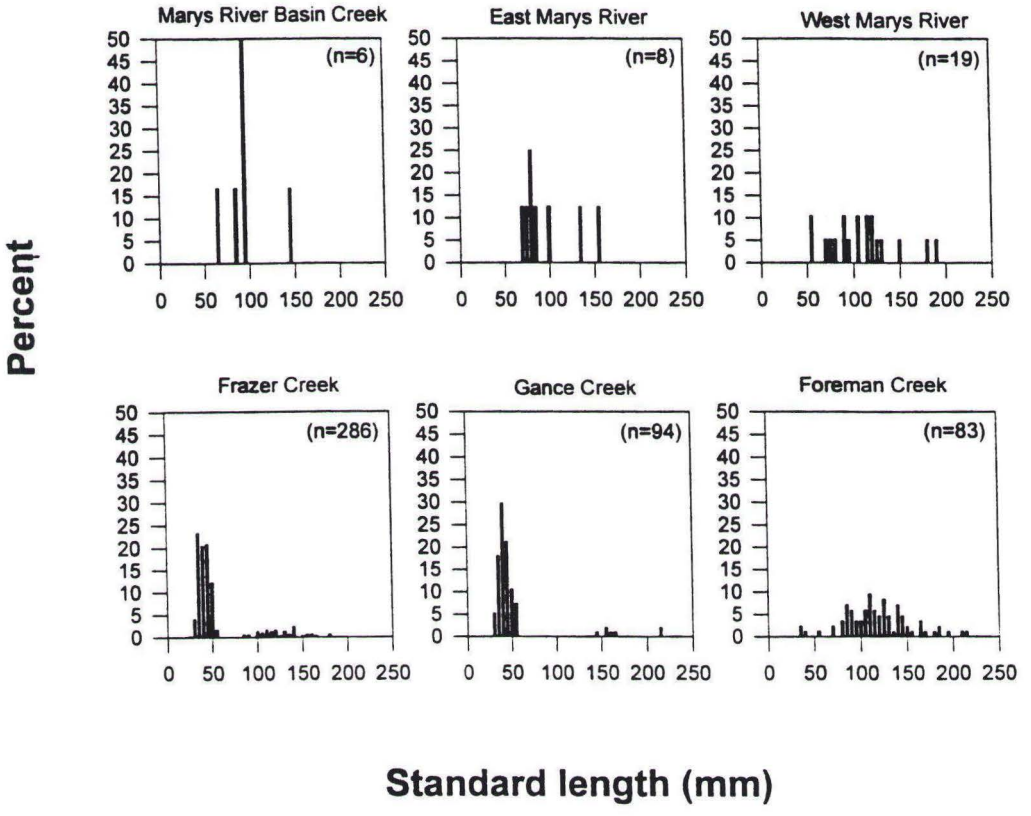

Marys River Basin Creek
(n=6)
East Marys River
(n=8)
West Marys River
(n=19)
Frazer Creek
(n=286)
Gance Creek
(n=94)
Foreman Creek
(n=83)
Percent
Standard length (mm)

Figure 4.

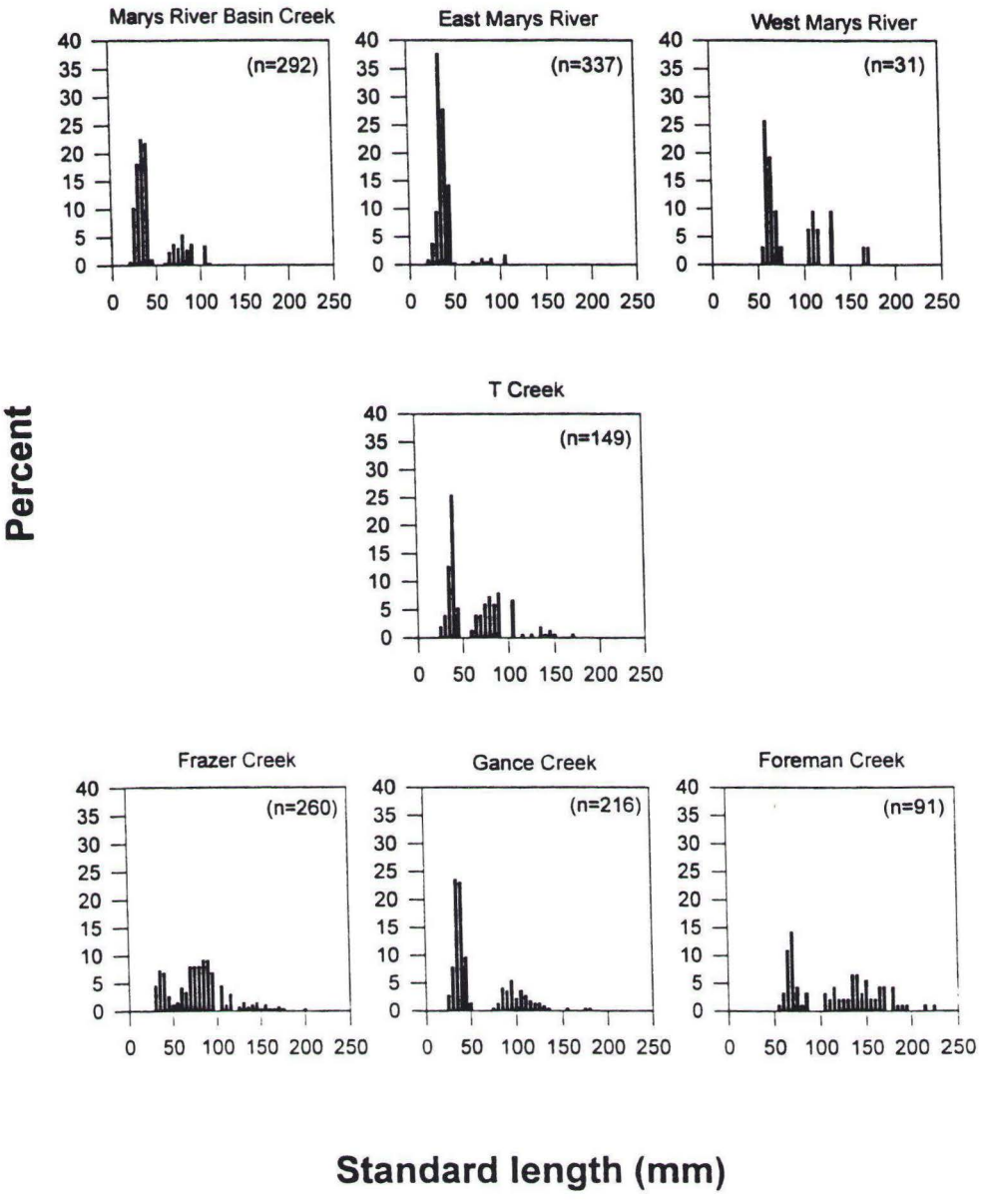
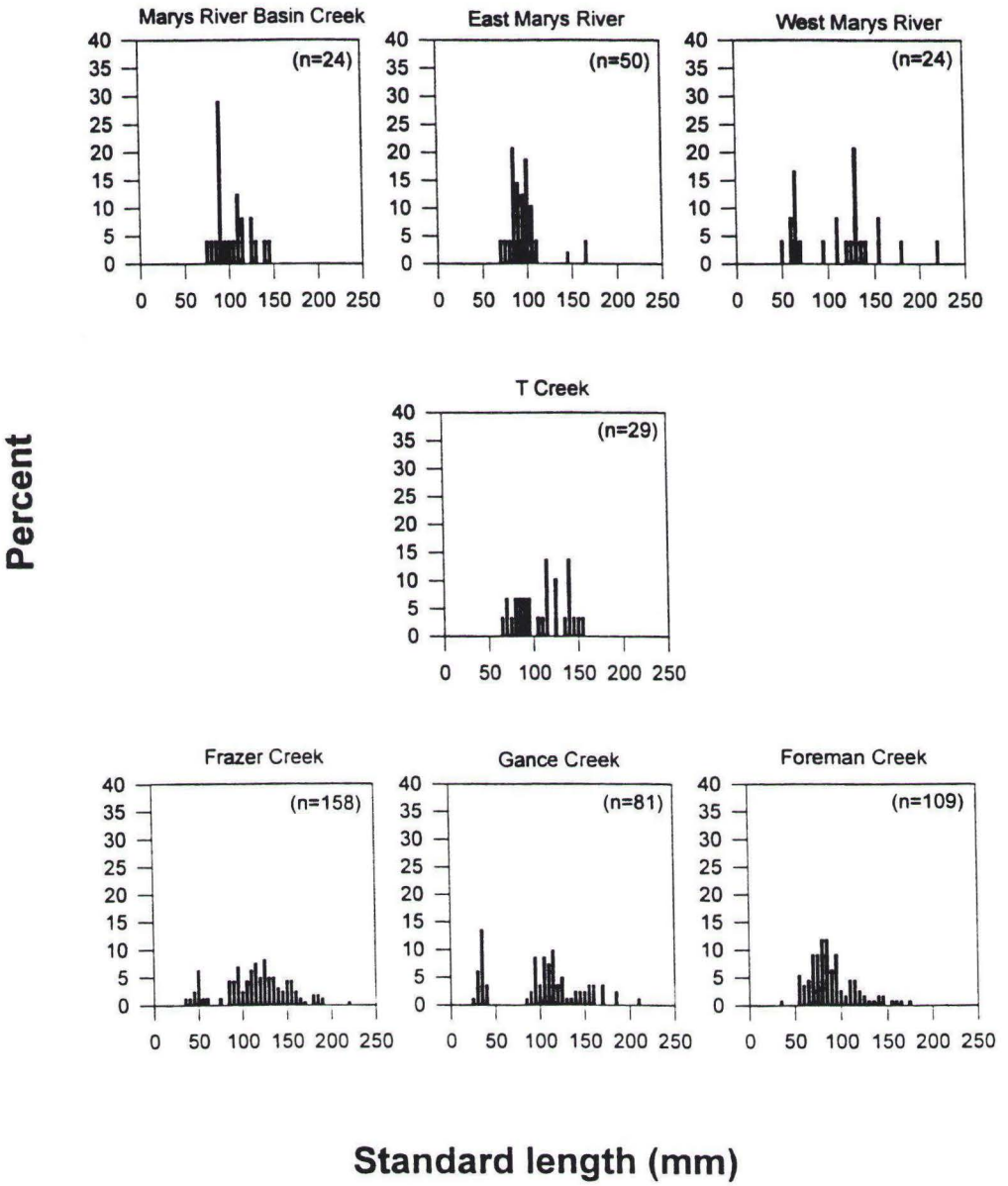

Marys River Basin Creek
(n=292)
East Marys River
(n=337)
West Marys River
(n=31)
T Creek
(n=149)
Frazer Creek
(n=260)
Gance Creek
(n=216)
Foreman Creek
(n=91)
Percent
Standard length (mm)

Figure 5.


Marys River Basin Creek
(n=24)
East Marys River
(n=50)
West Marys River
(n=24)
T Creek
(n=29)
Frazer Creek
(n=158)
Gance Creek
(n=81)
Foreman Creek
(n=109)
Percent
Standard length (mm)

Chapter 2.

Large-scale analysis of occurrence in a threatened trout

Abstract

Predictive models of species occurrence in subdivided habitats can be useful for parameterizing metapopulation models and for investigating factors that may be associated with local extinctions. The utility of species occurrence data for parameterizing metapopulation models has been demonstrated in some species. Constraints imposed by model assumptions, however, may limit their application to imperiled species that are in a non-equilibrium state with respect to regional and local environmental and demographic stochasticity. Here, we use species occurrence data to investigate factors associated with local extinctions in a "non-equilibrium" species, the Lahontan cutthroat trout (Oncorhynchus clarki henshawi).

In the past 150 years, Lahontan cutthroat trout have been extirpated from about 90% of their original stream habitats in the eastern Lahontan basin of Nevada. We used occurrence data collected by the Nevada Division of Wildlife (NDOW) to analyze cutthroat presence or absence in relation to habitat fragmentation, habitat size and shape, presence or absence of exotic salmonids, elevation and precipitation regime for 119 stream basins in the eastern Lahontan basin. We used random geographic coordinates to sample stream basins, but found that streams with data from NDOW surveys were likely a non-random sample of all streams formerly inhabited by Lahontan cutthroat trout. We thus restricted inferences from this analysis to the population of streams sampled by NDOW.

Multiple logistic regression analysis revealed a single factor, stream basin isolation, to be the only significant correlate of Lahontan cutthroat trout occurrence. Eighty-seven percent of stream basins connected to another basin containing Lahontan cutthroat trout also supported cutthroat trout, while only 31% isolated stream basins supported cutthroat trout. Overall, Lahontan cutthroat trout were found to occur in 56 (47%) of the 119 stream basins in this study.

The fact that stream basin isolation alone, and not factors such as stream basin area or presence or absence of exotic salmonids, were associated with Lahontan cutthroat trout occurrence, highlights the negative impact of habitat fragmentation on this threatened species. Further study is needed to more clearly establish the generality of this result, but this study supports the conclusions of more intensive, smaller-scale studies of Lahontan cutthroat trout in fragmented and interconnected stream basins. This result demonstrates the utility of simple presence-absence data for (1) studying potential factors associated with local extinctions, and (2) directing research questions on imperiled species.

Introduction

The ever-expanding number of imperiled species and the need to identify factors causing their decline is a major burden to conservation scientists and managers, who must address urgent conservation problems with limited financial resources and time. Detailed autecological data required for quantitative analysis of factors affecting population persistence are expensive and difficult to collect, and current methods of analysis are controversial (Simberloff 1988, Boyce 1992, Caughley 1994, Harcourt 1994, 1995, Açkacaya et al. 1995). Such data are clearly needed, however, to develop a stronger link between conservation theory and practice (Caughley 1994). In contrast, data on species occurrence (presence or absence) patterns are much less expensive and easier to collect. While such data are less detailed, they have nonetheless proven extremely valuable in ecology and conservation biology (MacArthur and Wilson 1967, Diamond 1975, Connor and Simberloff 1984, Gilpin and Diamond 1984, Taylor 1991, Jackson et al. 1992, Hanski et al. 1996).

Simple predictive models of species occurrence in subdivided habitats have been developed in the context of metapopulation theory (Hanski 1992, 1994, Hanski et al. 1996). Recent applications of these models have demonstrated their usefulness in situations where detailed autecological data are not available (Hanski et al. 1996). Widespread application of such models is

hampered, however, by their requirement that metapopulations are in a stochastic steady state (Hanski 1992, Hanski et al. 1996).

Many, if not most imperiled species are likely in a non-equilibrium state with respect to regional and local environmental and demographic stochasticity. In such cases, data on species occurrence are still valuable for exploring factors associated with their decline (e.g. Rieman and McIntyre 1995). Here, we present results of a large-scale analysis of local extinctions in Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*), a subspecies of cutthroat trout federally listed as threatened (Allendorf and Leary 1988, Coffin and Cowan 1995).

Recent studies of Lahontan cutthroat trout indicate a large-scale perspective is necessary to understand the factors associated with local extinctions (Dunham 1996). We used multiple logistic regression to analyze the binary response (cutthroat presence or absence) in relation to habitat fragmentation, habitat size and shape, presence or absence of exotic salmonid fishes, elevation and precipitation regime for 119 stream basins in Nevada. Results of this analysis are used to 1) identify potentially important factors associated with local extinctions; 2) compare our results with similar studies on other imperiled salmonids (Rieman and McIntyre 1995, Dunham 1996).

Methods

Study area and organism

Lahontan cutthroat trout are endemic to the Lahontan basin, located in the northwest region of the Great Basin of northern Nevada, northeast California and southeast Oregon (Behnke 1992). The origin of this species dates back at least 30,000 years (Behnke and Zarn 1976), and perhaps back to the Pliocene (Taylor and Smith 1981). At this time, cutthroat had access to myriad stream habitats and large lakes in the basin. The most recent high stand of Pluvial Lake Lahontan occurred about 14,000 years ago, when the lake itself covered approximately 22,100 km^2 (La Rivers 1962, Benson et al. 1990). After this time, Lake Lahontan rapidly dessicated to present-day levels by about 8,000 years ago, isolating cutthroat populations in the eastern (Quinn and Humboldt River) basins from those in the western basins draining the eastern Sierra Nevada mountains (Loudenslager and Gall 1980, Behnke 1992). Behnke (1992) considers the eastern form of Lahontan cutthroat trout to be a unique subspecies, but no formal description has yet been published.

The geographic range of Lahontan cutthroat trout includes a broad diversity of habitats including cold, oligotrophic alpine and subalpine lakes and streams, and stream and lake habitats in the warmer interior deserts of the Lahontan basin (La Rivers 1962). In the last 150 years, Lahontan cutthroat trout have been virtually eliminated from the western Lahontan basin and currently persist in only about 10% of their original habitat in

the eastern Lahontan basin (Coffin and Cowan 1995). Loss of cutthroat populations has been attributed habitat loss and degradation, interactions with exotic salmonid fishes and overexploitation (Coffin and Cowan 1995). Most remaining populations persist in small, isolated stream habitats that were historically interconnected. Several lines of evidence indicate such habitat fragmentation has significantly affected the structure, dynamics and extinction risk of Lahontan cutthroat trout populations (Dunham 1996). Our study included Lahontan cutthroat trout stream habitats from the Quinn and Humboldt River systems in Nevada (Fig. 1).

Data collection and analysis

In summary, our methods were to 1) sample a large number of streams within the historic range of Lahontan cutthroat trout, 2) establish cutthroat presence or absence in each stream, 3) collect data on physical and biotic characteristics of each stream, and 4) analyze cutthroat occurrence in relation to these characteristics.

Stream sampling. Streams in the eastern Lahontan basin of Nevada (Fig. 1) were randomly sampled (without replacement). With the exception of a single stream surveyed by us (JBD, pers. obs.), only streams surveyed by the Nevada Division of Wildlife (NDOW) were included in the analysis. As discussed below (see **Results**), the sample of streams sampled by NDOW was likely not a random sample of all habitats historically occupied by Lahontan

cutthroat trout. A total of 119 streams were included in this study.

Cutthroat occurrence. Lahontan cutthroat trout occurrence in the Quinn and Humboldt River systems (Fig. 1) was established with data from extensive surveys by NDOW biologists. Cutthroat occurrence and extinctions also were inferred from historical records (Snyder 1917; Coffin 1981, 1983; Trotter 1987, Gerstung 1988, Coffin and Cowan 1995), and data reviews by five experienced NDOW biologists (see **Acknowledgements**). Since Lahontan cutthroat trout have been extirpated from about 90% of their original stream habitats in the last 150 years (Coffin and Cowan 1995), we assumed most cutthroat absences reflect extinctions that occurred within this time frame.

In a few cases, determination of cutthroat occurrence was complicated by hybridization of cutthroat with rainbow trout (Oncorhynchus mykiss). If introgressive hybrization was suspected, we adopted the conservative philosophy of Dowling and Childs (1992), and scored such populations as Lahontan cutthroat trout. Unpublished reports of genetic studies contracted by NDOW generally indicate very low levels of introgressive hybridization in Lahontan cutthroat trout from the eastern Lahontan basins (Coffin and Cowan 1995).

Environmental variables. It was not possible to directly examine the impacts of land uses (e.g. livestock grazing, dewatering, mining) implicated in the destruction of Lahontan cutthroat trout habitat because they are difficult to quantify

and may require extensive (and expensive) sampling to sort out natural and anthropogenic impacts (Platts and Nelson 1988, Brussard et al. 1994). In addition, the impacts of land uses in the past (i.e. within the last 150 years) may not be observable in the present. Other factors that may extirpate fish populations in the Great Basin include fires (Minshall et al. 1989), floods and associated debris flows (Seegrist and Gard 1972, Erman et al. 1988, Sada 1990, Strange et al. 1992), droughts and high water temperatures (Keleher and Rahel 1996), freezing in winter (Nelson et al. 1992), interactions with exotic salmonids (Griffith 1988, Coffin and Cowan 1995), and habitat fragmentation (Rieman and McIntyre 1993, 1995, Dunham 1996). In general, the negative effects of these factors on fish populations are exacerbated by destructive land uses (Meehan 1991). Physical and biotic habitat variables with known relationships to environmental conditions that may affect fish population persistence were measured from maps or from existing data sets (Table 1).

Physical and biotic habitat variables measured for each stream included several geomorphic descriptors of basin shape previously shown to be related to flood characteristics of arid streams (Morisawa 1958, Murphey et al. 1977, Gordon et al. 1992, Table 1). Basin elevation (maximum, minimum, average) and precipitation characteristics of the stream basins were obtained from topographic and climatological maps (Table 1). Presence or absence of exotic salmonids was established from NDOW survey

records and reviews by agency biologists. No other exotic fishes known from Nevada, including centrachids, ictalurids or cyprinids (La Rivers 1962) were found in the streams.

Stream basin areas were estimated by digitizing topographic maps (Table 1). The lower (downstream) limit of a stream basin was defined as the point at which a stream joined an equal ordinal rank (stream order: Horton 1945), or by the 1500 meter elevational contour. Records indicate 1500 meters to be the historic lower elevational limit of stream-living Lahontan cutthroat trout in the Humboldt and Quinn River systems (Snyder 1917; J. Curran, NDOW pers. comm.). Here, we use the term 'historic' in reference to conditions that existed approximately 150 years ago, before white settlers colonized the Lahontan basin in the mid-19th century.

Cutthroat occurrence was analyzed in relation to physical and environmental habitat variation with multiple logistic regression (Aldrich and Nelson 1984, Hosmer and Lemeshow 1989). All data analyses were conducted with the SAS LOGISTIC procedure (SAS Institute 1995).

Results

During the sampling process, we had to discard many streams because they had not been surveyed by NDOW. Streams surveyed by NDOW in the past were generally selected if they were thought to have potential to support Lahontan cutthroat trout or a sport fishery for exotic fishes (Coffin 1983). This bias restricted

our sampling to higher elevation streams rather than all streams formerly occupied by Lahontan cutthroat trout. Accordingly, we restricted our inferences from the analysis to streams belonging to the population from which this sample was drawn.

Of the 119 streams selected, 56 (47%) were presently occupied by Lahontan cutthroat trout, 78 (66%) were occupied by exotic salmonids, including brook trout (*Salvelinus fontinalis*), rainbow trout (*Oncorhynchus mykiss*), and brown trout (*Salmo trutta*). Trout of any species were absent in 29 (24%) of the 119 streams. Physical environmental characteristics varied widely among stream basins (Table 2). For example, average elevation of the stream basins was 2275 m, and ranged from 1824 to 2860m, while stream basin size (area) averaged 80 km^2, and ranged from 2 to 1721 km^2 (Table 2).

All variables in the analysis (Table 1) were screened with best subsets logistic regression (SAS Institute 1995, Table 3). Only habitat fragmentation was found to be significantly related to cutthroat occurrence (Table 4). Overall, cutthroat were found to occur in 41 of 47 (87%) interconnected stream basins and only 22 of 72 (31%) fragmented stream basins. Possible interactions between habitat fragmentation and the other variables were examined, but only relief ratio, a measure of total basin relief (maximum - minimum basin elevation) in relation to stream basin area (Table 1), was found to interact (P=0.02) with habitat fragmentation. If this P-value is adjusted for the large number of statistical tests involved (n=12) with the sequential

Bonferroni method (Rice 1990), the resulting value is not significant (P=0.20). For this reason, we chose to ignore the Relief Ratio * Fragmentation interaction due to the high probability of type I error associated with multiple statistical comparisons (Rice 1990).

The logistic regression model equation from the analysis (Table 4) was:

$$\log(p_{\underline{LCT}}/1\text{-}p_{\underline{LCT}}) = -0.82 + 2.74x,$$

where $p_{\underline{LCT}}$ is the probability of Lahontan cutthroat trout occurrence given x, where x is whether or not a stream habitat is isolated (fragmentation: Table 1). Note that x is a binary category, and the logistic function is not smooth, but stepped in profile. Coefficients of determination estimated by a generalized R^2 and an adjusted R^2 (SAS Institute 1995) were 0.29 and 0.38, respectively.

Discussion

Results of this large-scale analysis of Lahontan cutthroat trout occurrence support the conclusions of other smaller-scale studies (Dunham 1996) and highlight the risk of extinction posed by habitat fragmentation and isolation of local populations in aquatic habitats (Zwick 1992). Isolation of local populations may increase the risk of extinction by causing loss of population

rescue by immigration and recolonization (Stacey and Taper 1992). In addition to isolation, habitat fragmentation reduces the size or area of remaining isolates (Harris 1984).

Reductions in habitat size may lead to loss of habitat complexity and life history variation, and reductions in population size; all of which may increase the risk of extinction (den Boer 1969; Harris 1984; Gilpin and Soulé 1987; Rieman and McIntyre 1993, 1995; Dunham 1996). Thus, habitat fragmentation may increase the risk of local extinctions through isolation and/or area-related effects, which may not be wholly independent (MacArthur and Wilson 1969).

Our finding that Lahontan cutthroat trout occurrence is related to habitat fragmentation alone, and not habitat size (stream basin area) or other factors suggests isolation-related effects are most important for the persistence of local populations - at least in regard to the predictor variables considered here. This contrasts with results of a similar analysis of bull trout (*Salvelinus confluentus*) in naturally fragmented habitats (Rieman and McIntyre 1995).

Lack of a relationship between cutthroat occurrence and factors such as habitat area and exotic salmonids was unexpected, since these are often the "usual suspects" implicated in the decline of native fishes (Miller et al. 1989, Minckley and Deacon 1991, Young 1995). Separate logistic regression analyses of Lahontan cutthroat trout in relation to rainbow, brook and brown trout failed to reveal significant relationships (JBD, unpubl.

data). The absence of a negative association between Lahontan cutthroat trout and rainbow trout, which may hybridize with the former, may possibly be explained by our decision to treat potential cutthroat X rainbow hybrids as occurrences (sensu Dowling and Childs 1992). However, genetic data on Lahontan cutthroat trout in the Humboldt and Quinn River basins indicate hybridization is not widespread (Coffin and Cowan 1995).

Our inability to detect a relationship between cutthroat occurrence and factors other than habitat fragmentation may be explained in several ways. Multiple agents of extinction, such as fires, floods, droughts, extreme temperatures, exotic species, destructive land use practices, overexploitation, and other factors all may affect population persistence of stream fishes. If many of these are operating to affect population persistence, it may be difficult to detect the individual effects of any specific factor. In other words, even with 119 streams in our study, we may not have enough statistical power to identify important causal agents of extinction.

Certain agents of extinction actually may have strong effects in individual basins, but only weak effects if considered across many streams affected by a variety of different factors. If multiple factors act sequentially or simultaneously, local extinctions may need to be considered on a case-specific basis. Furthermore, the impacts of various factors may function interactively, as in the extinction vortex concept (Gilpin and Soulé 1987, see also Simberloff 1988).

We found no associations between cutthroat occurrence and habitat area, but a similar study of another trout found occurrence to be positively related to habitat area (Rieman and McIntyre 1995). Differences between the results of this study and that by Rieman and McIntyre (1995) may be due to autecological differences between the two species, differences in the environmental conditions they experience, or both. For example, Rieman and McIntyre (1995) studied trout occurrence in naturally fragmented habitat patches. In contrast, Lahontan cutthroat trout habitats have been fragmented by human-related activities (Coffin and Cowan 1995). The degraded habitat conditions faced by many Lahontan cutthroat trout populations may have altered or reduced the relative impacts of area-related factors on their persistence. Habitat fragmentation resulting from natural processes, such as long-term hydrologic cycles in the Great Basin (Benson et al. 1990), has undoubtedly affected Lahontan cutthroat trout in the past, but fragmentation caused by human-related destruction of habitat may impact populations on much shorter time scales (Root and Schneider 1995). The response of fish populations to natural and human-caused habitat fragmentation may differ accordingly.

In summary, evidence from this and other (Dunham 1996) analyses of local extinctions in Lahontan cutthroat trout points strongly to the negative impacts of habitat fragmentation on the long-term viability of this species. Factors not directly measured in this study also may affect extinction risk in

cutthroat populations, and we caution that isolation alone is not necessarily a direct agent of extinction. Rather, isolation, by elimination among-habitat migration or dispersal and recolonization may lead to a ratchet-like pattern of local extinctions. Further sampling of stream habitats outside the range of those considered in this study may identify the impacts of other factors.

Incidence-functions have a relatively long history in ecology (Taylor 1991, Hanski 1992) and are becoming increasingly utilized in conservation biology (Hanski et al. 1996). Even if the equilibrium assumptions of currently available metapopulation models (Hanski 1992, 1994) do not apply (which often is the case), analysis of species' occurrence is a valuable tool for identifying important factors that may affect extinction risk. Incidence functions require only presence/absence data for a species, which is comparatively inexpensive to collect and may already be available in many cases. So long as the caveats of determining actual presence/absence are considered (Reed, in press), along with other sampling considerations (Taylor 1991, Hanski et al. 1996), incidence functions should prove to be a valuable tool in conservation biology.

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Table 1. Definition of variables considered in analyses of Lahontan cutthroat trout occurrence. See text for further detail.

Variable	Units	Derivation or definition
Total basin area	km^2	Digitized from US Geological Survey topographical maps.
Basin shape[1] factor	none	Square of maximum straight-line length of basin divided by total basin area.
Elongation ratio[2]	m^{-1}	Diameter of a circle with same area as that of the basin divided by total basin area.
Relief ratio[1]	m^{-1}	Total elevational relief (maximum-minimum elevation) divided by total basin area.
Average, maximum and minimum basin elevation	m	Estimated to nearest 40 m from US Geological Survey topographical maps.

Table 1. (cont.)

Variable	Units	Derivation or definition
Maximum precipitation[3]	cm	From precipitation contour maps of six hour, 100-year rainfall events.
Exotic salmonids	category	Scored as a 1 or 0 for presence or absence, respectively.
Fragmentation	category	Scored as a 1 or 0 depending on whether or not the basin was connected to another with Lahontan cutthroat trout.

[1]Sources: Murphey et al. (1977), [2]Morisawa (1958), and [3]US Department of Commerce (1973).

Table 2. Statistical summary of continuous habitat variables used in analyses of Lahontan cutthroat trout occurrence.

Variable	Mean (±std)[1]	CV (%)[2]	Range
Total basin area	80.31 (±188.87)	235.18	2.20-1721.01
Basin shape factor	4.47 (±4.04)	90.38	0.70-34.40
Elongation ratio	3.29 (±2.93)	89.06	0.48-20.72
Relief ratio	15.56 (±15.49)	99.55	0.37-88.39
Average elevation	2275.03 (±251.78)	11.07	1824-2860
Maximum elevation	2807.29 (±365.47)	13.19	2100-3588
Minimum elevation	1742.77 (±218.81)	12.56	1500-2400
Maximum precipitation	5.12 (±0.64)	12.54	4.07-6.10

[1]Standard deviation = (std).

[2]Coefficient of variation (CV) defined as (std/mean)·100.

Table 3. Results of best subsets variable selection for multiple logistic regression of Lahontan cutthroat presence/absence (for models with up to three variables). The two best combinations of explanatory variables in each model were selected as determined by the score statistic (Hosmer and Lemeshow 1989).

Number of variables	Score statistic	Variables in model
1	36.68	Fragmentation
1	8.19	Minimum Elevation
2	39.03	Fragmentation, Relief Ratio
2	37.38	Fragmentation, Longitude
3	39.84	Fragmentation, Area, Relief Ratio
3	39.68	Fragmentation, Relief Ratio, Maximum Precipitation

Table 4. Results of logistic regression of Lahontan cutthroat trout presence/absence in relation to habitat fragmentation.

Variable	Parameter estimate	95% Confidence interval (U, L)[1]	*P*[2]
Intercept	-0.82	-1.34, -0.33	0.014
Fragmentation	2.74	1.81, 3.82	0.0012

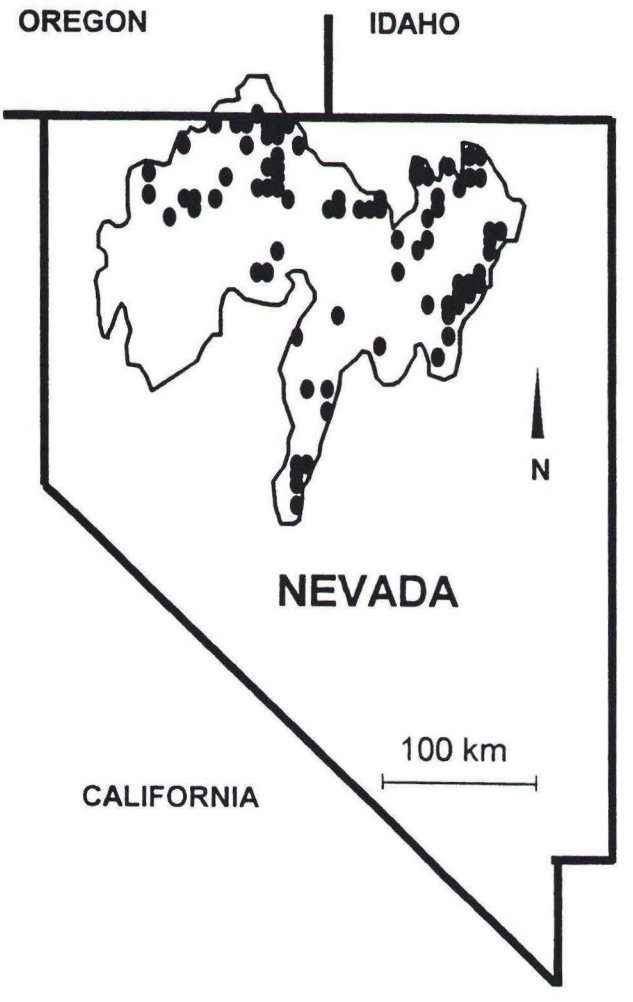
[1]Confidence intervals constructed from profile likelihood confidence limits (SAS Institute 1995), U and L refer to upper and lower 95% confidence intervals, respectively.

[2]*P*-value, from Wald chi-square statistic (SAS Institute 1995), adjusted for multiple comparisons with sequential Bonferroni method (Rice 1990).

Figure Caption.

Fig. 1. Geographic distribution of the 119 stream basins sampled (ovals) within the Humboldt and Quinn River basins of Nevada and southeast Oregon (solid outline).

Figure 1.



Chapter 3.

Relationships between body mass, population density, and the self-thinning rule in stream-living salmonids

Abstract: In food and/or space-limited populations, increases in average body size may be accompanied by increases in per-capita space and/or energy requirements. Thus, as body size increases in time or space, the maximum number of individuals that can be supported in a given environment should decrease. This relationship, referred to as self-thinning, produces a negative linear relationship between log body size (mass) and log population density. We studied body mass-population density relationships in stream-living populations of several trout species from the intermountain western United States. Our analyses of relationships between body mass and population density demonstrated that self-thinning can be manifested through both temporal and spatial variability in fish population characteristics. Several populations did not show self-thinning, possibly due to species-specific traits, temporal and spatial environmental variation, or both. Thinning lines may not reveal specific causal mechanisms, but they appear to be real, density-dependent responses and thus offer a potentially useful method for studying fish populations. Experimental studies of self-thinning under more controlled conditions are needed, however, to clarify these issues and eliminate alternative explanations for body size-abundance relationships.

Introduction

Individual variation in body size has important implications for population structure and dynamics (Peters 1983, Werner and Gilliam 1984, Lomnicki 1988). In fishes, body size is related to a variety of ecologically important characteristics, including competitive ability, survivorship, fecundity, diet breadth and growth rate (Wootton 1990). Because larger individuals generally require more resources, the maximum number of individuals supported in a given environment (carrying capacity) should depend on average body size. The expected relationship between maximum (equilibrium) population density (N) and average body size (mass, W) is commonly expressed as:

[1] $$N = aW^{-b},$$

where a and b are constants referring to the intercept and slope, respectively, of the body mass-population density regression. When this pattern is observed within species, it is referred to as self-thinning, a result of intraspecific competition for limited resources. Self-thinning has been studied extensively in plants, but only recently has attention been directed at mobile animal populations (Begon et al. 1986, Fréchette and Lefaivre 1995).

Some of the best evidence for self-thinning in fish populations comes from studies of stream-living salmonids in northwest England (Grant 1993, Elliot 1993), southern Sweden (Bohlin et al. 1994) and experimental stream channels (Grant

1993). The existence of a self-thinning relationship implies some factor or combination of factors is acting to limit population density. Two factors, space and food, are thought to be of primary importance in limiting salmonid production in streams (Chapman 1966). Thinning lines (eq. 1) for stream-living salmonids limited by space (territoriality) are predicted to have a slope of about -0.93 (Grant and Kramer 1990, Grant 1993), while lines for food-limited populations are predicted to have a slope of approximately -0.88 (Bohlin et al. 1994). The territory size thinning line is an empirical estimate derived from the relationship between territory size and body mass (Grant and Kramer 1990, Grant 1993), while the food limitation line is based on the theoretical concept of 'energetic equivalence' (Damuth 1981, Nee et al. 1991, Bohlin et al. 1994). Because (as we show in this study) slopes of thinning lines predicted from food and space limitation are very similar, they may be difficult to distinguish in practice.

Energetic equivalence is based on the fact that per capita energetic requirements increase as body mass increases. This increase is not 1:1, however, because metabolic rate slows down as body mass increases. The relationship between body mass and metabolic rate is:

[2] $$M = aW^{b},$$

where M is metabolic rate (mg $O_2 \cdot hr^{-1}$), and a and b are regression parameter estimates (Glass 1969). According to the energetic equivalence hypothesis, slopes of relationships between

population density and average body mass should be the inverse of slopes relating metabolic rate and body mass (-*b*, see Bohlin et al. 1994 for further discussion). If this holds, the sum of individual energy requirements remains constant during self-thinning (= energetic 'equivalence'). In other words, total energy flow through a population is independent of population density. This is expected if fish populations are limited by constant energy (food) inputs.

Slopes of thinning lines in stream-living salmonid populations studied to date generally are consistent with the energetic equivalence prediction (Grant 1993, Elliot 1993, Bohlin et al. 1994), thus it appears that food, rather than space limitation is more common (but see Keeley and Grant 1995). In this paper, we further investigate evidence for energetic equivalence in stream-living salmonids and attempt to identify important factors that may explain empirical deviations from its predictions.

Data used in this study come from intensive surveys of Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) populations in Great Basin (USA) streams and from long-term population surveys of resident trout throughout the intermountain region of the western United States (Platts and Nelson 1988). We studied relationships between body mass and population density to 1) look for the existence of thinning lines in these data sets, 2) examine the evidence for food and/or space limitation, and 3) examine spatial and temporal variation in self-thinning. To

explicitly test for independence of energy flow through a population and population density, we compared a regression model of population energy flow based on average body mass to an individual-based method.

Materials and methods

Study sites

Study areas for long-term population surveys are described by Platts and Nelson (1988). Field surveys of Lahontan cutthroat trout were conducted during the summers of 1993-94 in tributaries of the upper Humboldt River, Humboldt and Elko counties, Nevada. Streams ranged in elevation from 1700-2300 m. Average water depths in study areas were generally 15 cm or less, while wetted stream channel widths averaged 1 to 4 m. Stream conditions in this region are highly variable in space and time (Platts and Nelson 1988, Nelson et al. 1992). Winter conditions are often severe, with cold temperatures, anchor ice and avalanches at higher elevations. In some years, heavy spring runoff leads to severe flooding, which may directly kill or displace fishes (Seegrist and Gard 1972, Erman et al. 1988, Strange et al. 1992). Summer air temperatures often exceed 30°C, with daily water temperature fluctuations of up to 20°C. Drought conditions in 1994 led to extensive stream drying and fish mortality in areas just downstream of several study sites (Dunham and Vinyard, pers. obs.). Other fish species, including Tahoe sucker (*Catostomus tahoensis*), speckled dace (*Rhinichthys osculus*), and Piute

sculpin (*Cottus beldingi*) occurred in the study streams, but Lahontan cutthroat trout were generally the numerically dominant fish species present.

Sampling methods

In both data sets (long-term and Lahontan cutthroat trout), fish populations were sampled by electrofishing and population estimates obtained from multiple-pass depletions (van Deventer and Platts 1989). Details of sampling methods for long-term surveys were given in Platts and Nelson (1988). We used survey data from Platts and Nelson (1988) that spanned at least five years with areal biomass estimates consistently greater than 0.1 $g \cdot m^{-2}$.

Lahontan cutthroat trout data came from surveys of abundance at 42 sites in six streams in 1993 and 49 sites in seven streams in 1994 (n=7 sites per stream). Sites without fish were dropped from the analysis. When possible, the same sites were sampled in each year. Each site consisted of an approximately 25 m stream reach blocked at up- and down-stream ends with fine-mesh (3-4 mm diameter) seines to prevent fish escape during sampling. As with the long-term data (Platts and Nelson 1988), fish population density was expressed as number per unit area. Population estimates were obtained separately for young-of-year (age 0) and older (age 1+) fish. All sampling was conducted during summer base flow conditions (late July-September).

Statistical analyses

Body mass-abundance regressions

We analyzed body mass-abundance using ordinary least squares and reduced major axis (RMA, McArdle 1988) regression with population density (N) as the response and average body size (W) as a predictor variable with categorical stream effects in the model (Myers 1990). Abundance data from Platts and Nelson (1988) included several salmonid species (bull trout, *Salvelinus confluentus*; brook trout, *S. fontinalis*; Lahontan cutthroat trout *Oncorhynchus clarki*; rainbow trout, *O. mykiss*; and brown trout, *Salmo trutta*) in several streams. Stream and species effects could not be distinguished, so data were analyzed with a combined species-stream categorical variable to simultaneously account for species and stream effects. Data were analysed with the SAS General Linear Models procedure (Littell et al. 1991). Data were $\log_{10}$ transformed to linearize the relationship:

$$\log(N) = \log(a) - b\log(W)$$

with terms as defined above.

The first step in the analysis was to ensure model assumptions were satisfied. Residuals were obtained from the linearized statistical model and examined for normality with the SAS Univariate procedure (Littell et al. 1991). Output indicated studentized residuals were normally distributed, but a Levene's test (Kuehl 1994) on the absolute residuals indicated significant variance heterogeneity in the Lahontan cutthroat trout data. Because the models tested here are based on log-log relationships

between body size and abundance, we did not attempt further transformations. Instead, a weighted analysis was conducted by using $1/\sigma_i^2$ for body size at the jth site in stream i, following recommendations in Myers (1990) and Littell et al. (1991). This was necessary for both body-size abundance analyses and analyses of energy flow in relation to population density for Lahontan cutthroat trout (see **Population energy flow** below).

A preliminary analysis indicated (species-stream)*body size interactions were significant ($P<0.05$) in the long-term dataset, so slopes and intercepts were determined separately for each population. Stream*body size interactions were not significant ($P>0.20$) for the Lahontan cutthroat trout data, so the interaction term was dropped and the analysis was run again to estimate slopes.

Population energy flow

According to the hypothesis of energetic equivalence, population energy flow should be independent of population density. Thus far, theoretical arguments about relationships between body size and population density have been based on the relationship between *average* body mass and abundance. If the distribution of body sizes has a large variance or is substantially skewed, then average body size may poorly represent total energy flow in a population or community (Cyr and Pace 1993). If there is no size variation among individuals, overall energy flow through a population, F, is represented as:

[3] $$F = a\ W^{b} \cdot N,$$

the product of average mass-specific energy requirements ($a\ W^{b}$) and population density (fish·m^{-2}). If, however, there is substantial variation in the distribution of body sizes then overall energy flow through a population is more correctly specified as the sum of individual energy requirements. Taking w as individual body mass and summing for $i = 1$ to n, the number of individuals in a population, total energy flow may be calculated as follows:

[4] $$F = \Sigma\ a\ w^{b} \cdot m^{-2}$$

This formulation is more realistic for populations with large variation or skewed distribution in body size, as is often the case for species with Type III survivorship (e.g. fishes). Note in this case total energy flow (F) is expressed in units of mg $O_2 \cdot hr^{-1} \cdot m^{-2}$, which may be converted to energetic equivalents (Elliot and Davison 1975).

To compare the influence of underlying size frequency distributions on the relationship between body size and population density, we compared regressions of estimated total energy flow calculated from averages and from individuals versus population density. Total energy flow based on average and individual body mass was estimated as described above, and analyzed in relation to population density using the log-transformed linear model. Total energy flow was estimated using constants for *O. nerka*, obtained by Brett (1965). Differences between actual numbers of fish captured and population estimates

(van Deventer and Platts 1989) were generally very small (<10%). In cases where population estimates exceeded the number of fish captured, energy flow based on individuals was calculated by substituting average body size in place of the uncaptured individuals at each site. Average body size was calculated separately for young-of-year (age 0) and older fish (age 1+), and multiplied by the number of uncaptured individuals in the corresponding size class to estimate total energy flow.

Results

Body size-abundance

For the long-term dataset, multiple regression with body mass and the composite species-stream categorical variable explained approximately 90% of the variance in population density (Table 1). The moderately strong interaction between body mass and species-stream indicates the slope of the relationship between body size and abundance depends on stream effects, species effects, or a combination of both. For the 1993 Lahontan cutthroat trout data, multiple regression similarly indicated a weak, but significant stream*body size interaction effect (F=2.96, P<0.03, df=5), and significant stream effects (F=7.17, P<0.0003, df=5), but no significant effect of body size alone (overall model R^2=0.87). Body size was highly significant for the 1994 Lahontan cutthroat trout data (F=40.79, P<0.0001, df=1), with significant stream effects as well (F=15.62, P<0.0001, df=5), but no significant stream*body size interaction (i.e.

among-stream differences in regression slopes could not be distinguished). Together, body size and stream effects explained 80% of the variance in population density in 1994 (R^2=0.81).

Of the nine species-stream ordinary least squares slope estimates (b_{OLS}) in the long-term data (Fig. 1), four were found to be statistically significant (Table 2). With the exception of the RMA slope estimate (b_{RMA}) for bull trout, 95% confidence intervals around b included values predicted by the energetic equivalence and territory limitation hypotheses. The ordinary least-squares slope of the body size-abundance regression for Lahontan cutthroat trout surveyed in 1994 was -0.99±0.26 (95% CI), while the RMA slope estimate was -1.10, with the 95% CI ranging from -1.12 to -0.90. The latter slope estimate is significantly steeper than slope predictions from food limitation (-0.88), but not different from the slope predicted by space limitation (-0.93).

Energy flow vs. population density

Self-thinning did not apply for Lahontan cutthroat trout sampled in 1993 (Fig. 2). As a consequence, we only considered data from 1994. Multiple regression with stream effects included in the model as above indicated no significant relationships between population density and energy flow estimated from averages and individuals for Lahontan cutthroat trout sampled in 1994. Probability (P) values from partial F-tests of population density

effects were 0.81 and 0.15 for energy flow estimated from averages and individuals, respectively.

Discussion

Results from this study are more equivocal than previous investigations of self-thinning in stream-living salmonids (Grant and Kramer 1990, Grant 1993, Elliot 1993, Bohlin et al. 1994). Below, we discuss possible reasons for differences between our results and those from previous studies and briefly discuss what we view as important and untested issues and assumptions that must be addressed before self-thinning is widely accepted as a real phenomenon.

Evidence for self-thinning

Combined evidence from this study and others (Grant 1993, Elliot 1993, Bohlin et al. 1994) suggests self-thinning may occur in stream-living salmonids, but exceptions here require further explanation. In the long-term dataset, several species-stream combinations did not show a significant self-thinning pattern (Table 2). Regression slopes for streams with bull, rainbow and brown trout all showed the pattern expected from self-thinning, while streams with Lahontan cutthroat trout and brook trout did not. The consistent lack of a self-thinning pattern for brook trout is especially noticeable, with 5-9 years of data from four different streams showing no relationship between average body mass and population density. If there are indeed species-

specific differences in body size-abundance relationships, perhaps these can be attributed to different habitat preferences and competitive interactions (Gard 1961, Rodríguez 1995). Alternatively, stream habitats in this study may not have supported brook trout populations at maximum density.

Abundance and energy flow

Our finding of no significant relationship between population density and energy flow estimated from averages or individuals suggests the use of averages in body size-abundance regressions did not bias our analyses supporting energetic equivalence for Lahontan cutthroat trout in 1994. In other words, food limitation appears to be operating to adjust population density in relation to per capita energy requirements such that energy flow remains constant. This assumes, of course, that food limitation is directly operating to limit populations (see **Defining causal mechanisms** below).

There are ecological, as well as statistical reasons for considering the underlying distribution of body sizes in body size-abundance analyses. Bohlin et al. (1994) correctly point out that ontogenetic changes in diet, mortality and growth may lead to *b*-values substantially different from those predicted by the hypothesis of energetic equivalence. Our datasets cover a relatively wide range of body sizes within and among streams, but overall homogeneity of slopes for streams with wide variation in

body size in the 1994 Lahontan cutthroat trout data suggest *b*-values are similar in this range.

Results from other studies of stream-living salmonids indicate ontogenetic dietary differences may not be as large as one might suspect. A recent study of dietary overlap in stream-living Colorado cutthroat trout (*O.c. pleuriticus*, Bozek et al. 1994) found considerable overlap in taxonomic composition and size of food items consumed by individuals ranging from 24 to 188 mm (total length), and that food items too large to be accomodated by the gape size of age 0 fish were rarely encountered. Mortality patterns also may not vary substantially for different size classes because all populations in this study were surveyed during low summer flows. Summer mortality in stream-living salmonids is generally low in comparison to winter and spring (Seegrist and Gard 1972, Strange et al. 1992, Hutchings 1993). However, during our studies of Lahontan cutthroat trout, large adults occasionally were observed acting aggressively toward smaller individuals. Thus, smaller individuals, especially (age 1 and younger) may be displaced to areas of higher predation risk and reduced growth.

Temporal vs. spatial variation

Confidence intervals for slopes and intercepts are much wider for the long-term data (Platts and Nelson 1988) than for the Lahontan cutthroat trout dataset. Since the former data were from annual surveys and the latter were from surveys conducted in a single

year, increased variability in the long-term data may reflect higher temporal variation in ecological factors affecting salmonid populations. The contrasting results for self-thinning in Lahontan cutthroat trout in 1993 and 1994 lead us to suspect environmental variation has a large temporal component. This also may explain why body mass-abundance regressions for Lahontan cutthroat trout were not significant in the long-term data. For this reason, we suggest parameter estimates for body mass-abundance regressions will be more precise when population data come from many sites sampled in a relatively narrow time period, as opposed to fewer sites sampled over longer (e.g. yearly) time periods.

Our data for Lahontan cutthroat trout include samples from Gance Creek, Nevada, also sampled by Platts and Nelson (1988). Their eight years of annual survey data in Gance Creek show no evidence of self-thinning for Lahontan cutthroat trout, but our data show a strong self-thinning pattern for 1994, but not 1993. The significant stream*body size interaction observed in 1993 was probably due to the strong, negative relationship between body mass and population density in Frazer Creek (Fig. 2). Other streams sampled in 1993 give little indication of such a relationship (Fig. 2).

We suspect differences between these two years are related to variation in stream discharge. Data collected by U.S. Geological Survey in the upper Humboldt River basin, Nevada (which includes Gance Creek) show that stream discharges in 1994

were among the lowest recorded in the last 50 years. Low water levels and reduced habitat volume may have caused an intraspecific competitive 'crunch' (sensu Weins 1977) during drought conditions of 1994. Differences between our data and that from Platts and Nelson (1988) are discussed in more detail below.

Defining causal mechanisms

When populations in this study did show patterns expected with self-thinning, slopes of thinning lines were equally compatible with predictions from food (energetic equivalence) or space (territoriality) limitation. An exception was the Lahontan cutthroat trout data for 1994, where the b_{RMA} slope was consistent with space limitation, but significantly steeper than predicted by food limitation. Analyses of energy flow in relation to population density are consistent with food limitation, however. Our inability to distinguish between these two alternatives may stem from several related complications in the analysis of thinning lines.

First, predicted slopes from the food and space limitation hypotheses are very similar (~0.88 versus 0.93, respectively), so random error in estimates of body size and population density must be very small to effectively distinguish alternatives. Natural variability in environmental conditions also may increase variation around thinning lines, possibly affecting slopes and intercepts as well. It is well-known that temperature and

metabolic rate are closely coupled in fishes. For example, metabolic scaling exponents (*b* in eq. 2) for brown trout ranged from 0.92 to 1.15, depending on temperature (Beamish 1964, Glass 1969). Predicted slopes of thinning lines for food-limited brown trout populations thus range similarly as ambient temperatures vary. Other factors such as spatial and/or temporal variation in underwater visibility, habitat structure or physiochemical conditions may also affect behavioral interactions and metabolic rates. Finally, a recent analysis of this problem by Marschall and Crowder (1995) suggests food and space limitation may be theoretically indistinguishable.

Finally, we must mention our concerns with the use observational data and correlational analyses to examine thinning lines. In this study, we considered only body mass as a correlate of population density. Significant correlations between these variables may not be a direct result of causal relationships. This could be a problem for at least two important reasons. First, we have no direct, independent measure of food and/or space limitation. Second, body mass may be correlated with a third, unmeasured factor that also affects population density and thus may not be a direct causal agent. Before self-thinning becomes a widely accepted phenomenon, we emphasize the need for experimental studies under more controlled conditions (e.g. Begon et al. 1986, Latto 1994, Fréchette and Lefaivre 1995) to more clearly address these unresolved issues.

Even if specific mechanisms producing thinning lines are not fully understood, their existence implies that maximum population density in a given environment (carrying capacity) is body size-dependent. We have shown here that analysis of thinning lines may serve as an important tool for determining when populations are at carrying capacity and for comparing among-population variation in population density. Analysis of thinning lines may also identify habitats that favor fish of different body sizes. Bohlin et al. (1994) describe the effects of changing stage or body size-specific schedules of mortality (or emigration) and growth on the form (linear, curvilinear) and slopes of self-thinning lines. Study of self-thinning in these contexts should provide important new insights into the interactions between environmental variability and biotic and abiotic control of fish populations and commununites.

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Table 1. Analysis of variance table for multiple regression analysis of the long-term dataset (R^2=0.90).

Source	df	MS	*F*	*P*
Species*stream	8	0.167	4.69	0.0003
Average body mass	1	0.775	21.78	0.0001
Interaction	8	0.824	2.89	0.0109
Error	45	0.036		

Table 2. Parameter estimates and 95% confidence intervals for slopes from regression analyses of body size vs. abundance in the long-term dataset (Platts and Nelson 1988). Sample sizes (n) represent the number of annual surveys. P-values are for slopes (b_{OLS}). RMA slopes (b_{RMA}) were not estimated when least-squares were not significant (McArdle 1988).

Species (Locality)	b_{RMA} (95%CI)	b_{OLS} (±95%CI)	n	P
Bull trout (SF Salmon River)	-1.79 (-2.81, -1.13)	-1.40 (±1.02)	11	0.0033
Rainbow trout (Tabor Creek)	-1.14 (-1.91, -0.69)	-1.06 (±0.60)	6	0.0001
Rainbow trout (Otter Creek)	-1.43 (-3.01, -0.68)	-1.28 (±1.17)	5	0.0006
Brown trout (Otter Creek)	-2.06 (-5.37, -0.80)	-1.65 (±1.43)	5	0.0007
Brook trout (Johnson Creek)	- -	-0.19 (±1.23)	9	NS
Brook trout (Horton Creek)	- -	-0.02 (±1.09)	7	NS
Brook trout (Frenchman Creek)	- -	-0.34 (±0.86)	8	NS

(Continued)

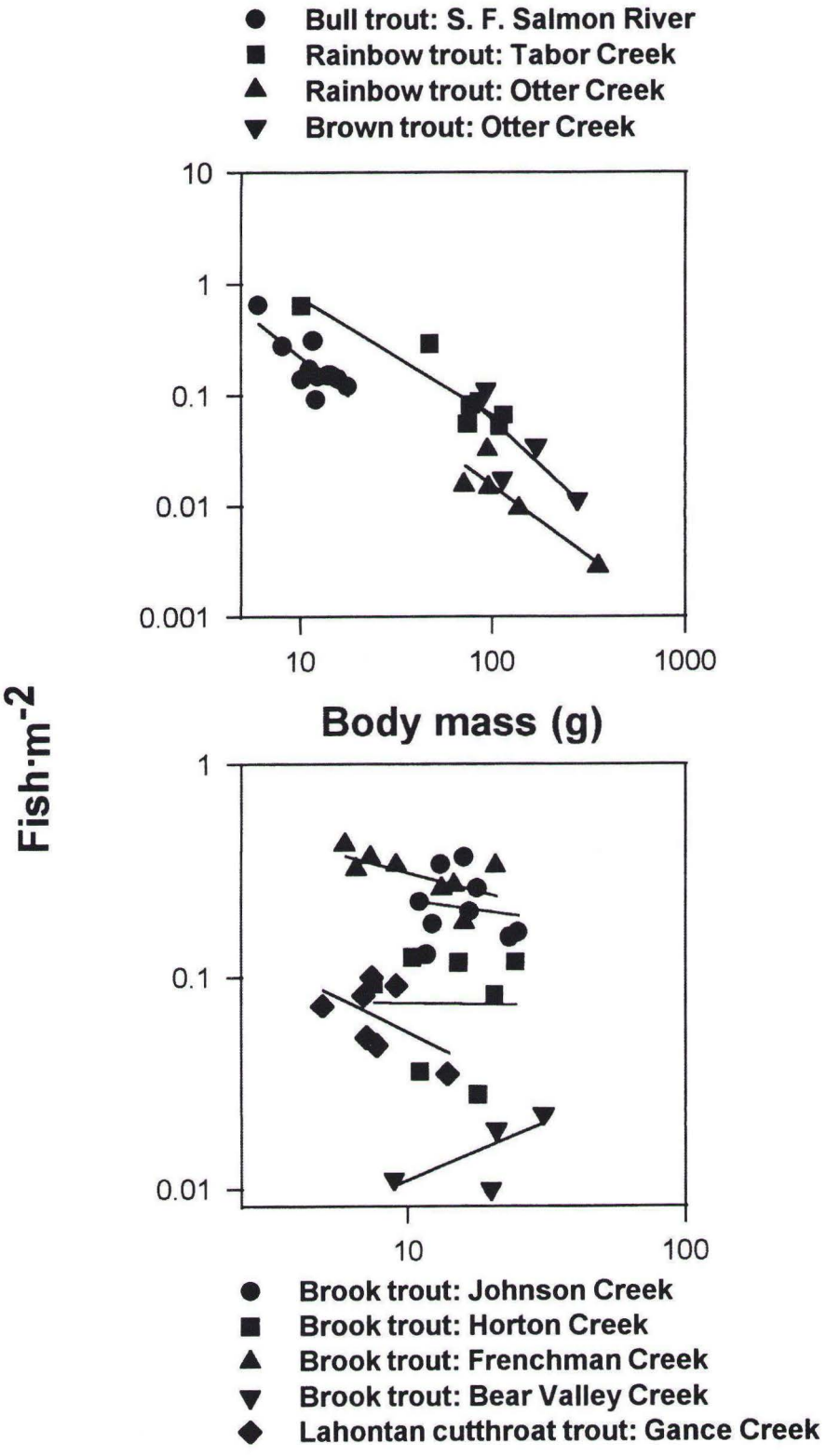
Table 2. (cont.)

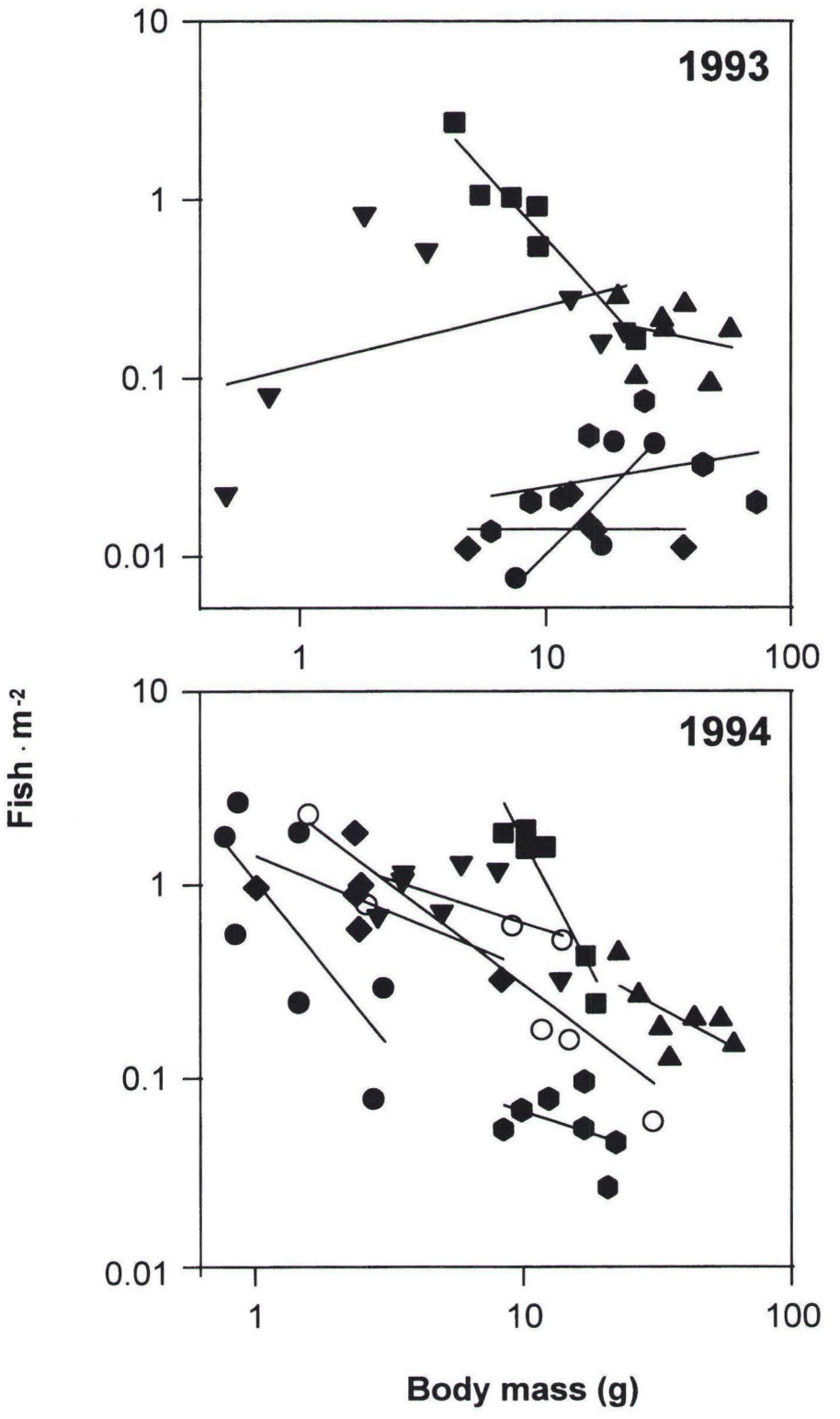
Species (Locality)	b_{RMA} (95%CI)	b_{OLS} (+95%CI)	n	P
Brook trout	-	0.54	5	NS
(Bear Valley Creek)	-	(±1.51)		
Cutthroat trout	-	-0.65	8	NS
(Gance Creek)	-	(+1.36)		

Figure captions

Fig. 1. Thinning lines for five salmonid species studied in nine streams (data from Platts and Nelson 1988). Each point represents one annual population estimate. Thinning lines with significant slopes (Table 2) are shown in the top graph, while those with non-significant slopes are in the bottom graph.

Fig. 2. Scatterplots of body mass-population density relationships for Lahontan cutthroat trout studied in six streams in 1993 and seven streams in 1994 (T Creek added in 1994). Each point represents a population estimate for one site. Regression lines are the weighted least-squares line for each population.


Bull trout: S. F. Salmon River
Rainbow trout: Tabor Creek
Rainbow trout: Otter Creek
Brown trout: Otter Creek
10
1
0.1
0.01
0.001
10
100
1000
Body mass (g)
Fish·m-2
1
0.1
0.01
10
100
Brook trout: Johnson Creek
Brook trout: Horton Creek
Brook trout: Frenchman Creek
Brook trout: Bear Valley Creek
Lahontan cutthroat trout: Gance Creek


1993
1994
10
1
0.1
0.01
1
10
100
Fish · m-2
Body mass (g)
T Creek
East Marys River
Marys River Basin Creek
Frazer Creek
Foreman Creek
West Marys River
Gance Creek

Chapter 4.

Incorporating Stream-Level Variability into Analyses of Site-Level Fish Habitat Relationships: Some Cautionary Examples

Abstract.-Spatial variation in stream fish populations and habitats can be partitioned into many hierarchical levels (e.g. among drainage basins, streams within basins and sites within streams). Studies of site-level habitat relationships in more than one stream are common in fisheries research. Analyses of such data typically involve multiple regression to relate site-level habitat features and fish population characteristics (e.g. biomass). Because sites within streams may not be independent, multiple regression models should also include qualitative stream effects. As we show here with hypothetical and real examples, ignoring stream effects can lead to erroneous conclusions about the significance of site-level habitat variables. Site and stream-level effects may function independently or interactively in relation to fish populations. It may also be the case that site and stream-level effects cannot be distinguished. An example with data on trout populations revealed that highly significant site-level effects were only marginally significant after adding qualitative stream effects to the regression model. Further examination of the data revealed that consideration of among-stream variation added much insight and complexity to understanding how site-level effects may be related to trout populations. Inclusion of stream (or other large-scale) effects in regression models of site-level habitat relationships may be a valuable method to more fully understand the spatial scale of habitat variability fish are responding to.

Introduction

Answers to ecological questions are often scale-dependent (Wiens et al. 1986, May 1994, Root and Schneider 1995, Wu and Loucks 1995). In this regard, studies of relationships between stream fishes and habitat variables (Fausch et al. 1988) are no exception. Stream fish habitat relationships have been examined at a variety of spatial and temporal scales (e.g. Frissell et al. 1986, Baltz 1991, Bozek and Hubert 1992, Strange et al. 1992, Hawkins et al. 1993, Matthews et al. 1993), but the impracticality of considering all relevant spatial and temporal scales is an unavoidable constraint. Here, we briefly consider one aspect of this problem: within-stream versus among-stream variation in studies of relationships between habitat variation and fish populations.

Spatial variation in fish populations and habitats can be hierarchically partitioned into variability among drainage basins, among streams within drainages, within streams, and so on (see Frissell et al. 1986, Hawkins et al. 1993). Surveys of fish populations at sites within several streams are thus measuring variability due to site-level and stream-level effects. This particular survey design is common in fisheries research (e.g. Fausch et al. 1988). Investigators typically use multiple regression models to relate site-level habitat variables to fish population characteristics (Fausch et al. 1988). Stream-level effects are often ignored in the analysis of this type of data.

It may be that data on stream-level variables are lacking, but specific information is not necessary to statistically test for stream effects. Below, we show how ignoring stream effects can bias results of analyses of site-level habitat relationships and offer simple advice on how to better design and analyze such studies.

Methods

Rather than criticize the work of others, we will consider a hypothetical example and then utilize original data to show how both stream and site-level variation are relevant. Since fish habitat studies commonly use multiple linear regression (Fausch et al. 1988), we will emphasize this statistical method (see Manly 1986 for alternatives). The uses of regression analysis fall into several categories (Myers 1990), including prediction of a response (e.g. prediction of fish population characteristics in relation to environmental variation), variable screening (e.g. to determine which environmental variables are most strongly related to fish populations), model specification (e.g. to determine the form of the relationship between fish populations and environmental variation) and parameter estimation (e.g. to determine the slopes or intercepts of the relationships between environmental variables and fish population characteristics). In the examples that follow, we will emphasize variable screening as our general objective. Our point here is <u>not</u> to define specific

causal mechanisms that affect fish populations, but rather to look for important patterns of variation in an exploratory analysis.

Regression models with a categorical (also called class, indicator, dummy, treatment, design, or qualitative) variable, such as "stream" and one quantitative regressor variable take the following form:

$$y_i = \beta_0 + \beta_1 x_i + \epsilon_i \quad (1)$$

for category 1, and

$$y_i = (\beta_0 + \beta_2) + \beta_1 x_i + \epsilon_i \quad (2)$$

for category 2 (and so on, for each category), where y_i is the measured response variable for the i^{th} observation, β_0 is the y intercept, β_2 is the intercept difference between category 1 and 2, and β_1, x_i, ϵ_i are the slope, measured predictor variable and random error, respectively (see Myers 1990 for extensions of this simple model). In the examples that follow, β_0 represents stream effects and β_1 is the slope relating site-level variation (x_i) to fish biomass (y_i).

Regression analyses with qualitative and quantitative regressors belong to a general class of linear statistical models that includes analysis of variance (ANOVA) and analysis of covariance (ANCOVA) (Neter et al. 1985, Myers 1990, Littell et al. 1991). In other words, regression models with one or more quantitative regressors and one or more categorical variables are statistically identical to ANCOVA models, where the quantitative regressors are viewed as covariates. The term ANCOVA implies the

quantitative regressors are not of direct interest to the study, but used to adjust the treatment means (mean values for each stream, in this case) in relation to the covariate(s) (site-level variables in this case) (see Kuehl 1994).

Hypothetical examples

We initially consider hypothetical data with three stream categories and six sites per stream to illustrate five possible types of relationships between fish populations (e.g. biomass) and stream-level and site-level variation (Fig. 1). Similar examples can be found in Myers (1990) and Neter et al. (1985). First, it is possible that both stream and site-level effects are significant, but independent (i.e. equal slopes with different intercepts; Fig. 1a). Alternatively, only site-level (intercepts and slopes equal; Fig. 1b) or stream-level (different intercepts, slopes not significant; Fig. 1c) effects may be important. Stream-level and site-level effects may also be interactive (i.e. slope depends on stream; Fig. 1d) or confounded (stream and site effects cannot be distinguished; Fig. 1e). The sixth possibility is the null case in which fish populations and habitat are not related at any level (Fig. 1f). The point here is that 4 of 6 possibilities involve stream-level effects. From these simple examples, it is clear that stream-level effects may be important in analyses of relationships among site-level variation and fish population characteristics.

A Real World example

To further illustrate these possibilities, we used data from surveys of Lahontan cutthroat trout (Oncorhynchus clarki henshawi) abundance and several site-level habitat variables at 49 sites in seven headwater streams in the upper Humboldt River drainage, northeast Nevada (Dunham and Vinyard, unpubl. data). Four streams (West Marys River, East Marys River, Marys River Basin Creek) are perenially interconnected tributaries of the upper Marys River, while T, Foreman, Gance and Frazer Creeks are isolated stream habitats. Catchment basin areas and average elevations of these streams range from 13 to 27 km^2 and 1975 to 2670 m, respectively.

All streams were sampled within a very short (1.5 mo) time period during summer base flow to minimize temporal differences (cf Austen et al. 1994). In each stream, we surveyed seven approximately 25 meter sections of stream with multiple-pass electrofishing (van Deventer and Platts 1989). Two stream sites were dropped from the analysis because cutthroat were absent for reasons unrelated to habitat conditions (e.g. physical migration barriers). Habitat variables measured at each site included average water depth, maximum water depth, wetted channel width, numbers of large woody debris pieces, canopy density, undercut bank volume, instream macrophyte and woody cover, conductivity, and pH. Details of this work will be published elsewhere.

Multiple regression analyses were conducted with SAS (Freund and Littell 1991, Littell et al. 1991) to examine relationships between $\log_{10}$ cutthroat biomass (g fish·m^{-1}) and site-level habitat variables. Logarithmic transformation of the response was needed to stabilize variance heterogeneity (tested with ANOVA on the absolute residuals; Kuehl 1994), and to linearize relationships between biomass and the regressor variables (determined by examination of partial regression plots; Myers 1990). We selected the best linear regression model using "all subsets" regression (SAS PROC REG RSQUARE option; Littell and Freund 1991). Model selection criteria included mean square error, Mallows' C_p, R^2 and adjusted R^2, which adjusts for number of variables in the model (Myers 1990, Freund and Littell 1991). Multicollinearity, influential observations, variance heterogeneity and other diagnostics were evaluated to ensure model assumptions were satisfied (Phillipi 1994). Following variable selection, we re-analyzed the reduced model with stream effects included in the model as a categorical variable. Stream*site interactions were tested as well.

Results and Discussion

Model selection criteria identified instream macrophyte cover and wetted stream width as the two best site-level predictor variables. With these two site-level variables, we investigated four models corresponding to possible fish habitat

relationships shown in Fig. 1a-d (Table 2). To look at site effects only (Fig. 1b), we conducted a separate multiple regression with stream width and instream macrophyte cover (Table 2a). Regression results indicated only width effects were significant ($P<0.0001$), so instream macrophyte cover was dropped from subsequent analyses. Analysis with a model including both width and stream effects (Table 2b, compare to Fig. 1a) showed strong stream effects ($P<0.0001$), but stream width was only weakly ($P=0.045$) related to cutthroat biomass. Stream*width interactions were not significant (Table 2c), but stream effects alone explained over 75% of the variation in cutthroat biomass. Adding stream width to the model only increased R^2 by three percent (from 0.75 to 0.78, Table 2b,d). If stream effects were ignored in this analysis, wetted width and cutthroat biomass would appear to be strongly related (Fig. 2), but our analysis with stream effects indicates biomass variation among streams is much greater than variation among sites within streams (width effects).

A closer examination of the plot of stream width versus fish biomass per meter (Fig. 2) shows our real world example is not as clear cut as the hypothetical examples (Fig. 1). The finding that stream-level effects dominate site-level (e.g. width) variation masks potentially more complex patterns in the data. Only two streams (West and East Marys Rivers) showed significant ($P<0.05$) negative width effects (regression slopes) when separate regressions were fitted for each stream. These streams (West

Marys River and East Marys River) appear to show within-stream width effects that correspond to the hypothetical example in Fig. 1a, or perhaps Fig. 1b, depending on intercept differences. Other streams show no such relationship. This type of overall pattern suggests a stream*width interaction, but interaction effects were too weak to be detected with a sample size of only 6-7 sites per stream.

In other streams shown in Fig. 2, stream width appears to be confounded with among-stream variation in biomass (Fig. 1e). For example, within-stream variation in fish biomass and stream width in Frazer, Gance, T, Foreman and Marys River Basin Creeks appear to vary together as a function of stream. In conclusion, it may be true that stream width is an important correlate (no causation implied) of fish biomass in the seven streams in this example, but addition of stream effects to the model reveals additional complexity that would not be apparent by an analysis of stream width (site effects) alone. In other words, if the data were analyzed by assuming only width (site) effects (see Fig. 1b, Table 1a), this complexity would be missed.

We emphasize the use of multiple linear regression here, but there are other related statistical methods available for detecting spatial structure in ecological datasets, such as spatial autocorrelation analysis (Legendre 1993, Hinch et al. 1994, Fortin and Gurevitch 1994). In terms of equations 1 and 2, autocorrelation refers to correlations among the error terms (ϵ_i) among sites within streams. Our example data set with Lahontan

cutthroat trout, consisting of only 6-7 sites per stream, was too small to test for autocorrelation with available methods (Fortin and Gurevitch 1994).

Positive spatial (and temporal) autocorrelation may not bias parameter estimates, but variances may be underestimated, inflating the chance of finding a significant result when in fact one does not exist: a type I statistical error (Zar 1984). In our example, we may expect positive spatial autocorrelation due to movement of individuals among sites or similar stream channel characteristics, for example (cf. Fortin and Gurevitch 1994).

A common remedy for dealing with autocorrelated errors is to add additional regressor variables to remove the autocorrelation (Myers 1990). The fact that site-level variability (i.e. stream width) was only marginally significant ($P<0.045$) after adding stream effects in the regression analysis suggests that autocorrelation may have been present.

Conclusion

Results of the above analyses strongly suggest cutthroat biomass is related to stream-level and possibly to site-level habitat variation (at least with respect to site-level variables measured in this study) as well. In some cases, the analyses suggest stream and site effects may be confounded. At this point, we know little about specific stream-level habitat characteristics, but at least we have a clearer idea of the

relevant spatial scales for addressing cutthroat habitat relationships (note here we are purposely ignoring the problem of using population density or biomass alone as an indicator of habitat quality; van Horne 1983).

An important caveat to note here is that analyses such as those described here to analyze stream effects, must use biologically meaningful definitions of "stream" or other such unit used in such analyses (e.g. "basin," "reach," or "channel unit," see Frissell et al. 1986). In our example with Lahontan cutthroat trout, streams in the analyses are meaningful units because they are either isolated from other fluvial habitats or tributary to larger mainstem habitats. In the latter case, we consider the tributary streams to be meaningful units because they have very different characteristics than their larger mainstem counterparts (Minshall et al. 1983).

A second important caveat of the approach we use here is that pattern detection methods, such as regression analysis, do not necessarily imply causal relationships. Such analyses may be essential, however, to the formation of causal hypotheses and more experimental, process-oriented study (Ludwig and Reynolds 1988). Our point here is not to discuss all of the potential larger-scale, stream-level processes that may actually affect stream fishes, but rather to show how site and stream-level variability may be considered together in a correlation or regression analysis. In our example, lack of specific information on exactly what stream effects (e.g. stream size,

elevation, geomorphology, or other characteristics) may be related to Lahontan cutthroat trout populations and how they may affect populations indicates larger-scale experimental and observational studies are needed to better understand this species.

To summarize, studies of site-level fish habitat relationships from sites in more than one stream should consider the following: 1) stream effects are potentially very important in developing habitat models to predict fish biomass; 2) interactions among stream and site-level variation may also be important; 3) inclusion of effects at different scales is useful for determining the scale of habitat variability (e.g. the "environmental grain," sensu Levins 1971) fish are responding to; 4) specific characteristics of streams need not be known to include stream effects in a habitat model; 5) sampling designs should include enough sites and streams to detect effects at different scales (Cohen 1977).

Lack of attention to stream (or other large-scale) effects may partly explain why habitat-based models often have little explanatory power (Fausch et al. 1988). Even worse, as evidenced by the examples presented here, failure to consider more than one spatial (or temporal) scale can lead to serious misinterpretations. We do not, however, wholly condemn habitat models based on limited spatial scales! Such information is very useful so long as inherent constraints of the data are acknowledged. Obviously, it is practically impossible to

consider all relevant spatial and temporal scales in studies of stream fish-habitat relationships. Nonetheless, as we have shown here, ignoring the problem of scale in fisheries can have serious consequences in a scale-dependent world.

Acknowledgements

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Table 1.-Analysis of variance tables for different models of relationships between Lahontan cutthroat trout biomass and stream- and site-level habitat variation for (a) multiple regression with two site-level predictor variables (R^2=0.62); (b) a model with qualitative stream effects and stream width (R^2=0.78); (c) same model as (b), but with a stream*width interaction in the model (R^2=0.80); (d) a model with stream effects only (R^2=0.75). Mean square (MS) values are from partial (SAS Type III) sums of squares, except for case (c), where MS values are from SAS Type I sums of squares (see Myers 1990, Littell et al. 1991)

Source	df	MS	*F*	*P*
Site effects only				
model	2	3.334	35.32	0.0001
Error	44	0.094		
Stream and site effects				
stream	6	0.323	5.25	0.0005
stream width	1	0.263	4.28	0.0451
Error	39	0.061		
Stream, site and stream*site interaction				
stream	6	1.360	21.22	0.0001
stream width	1	0.263	4.11	0.0507
interaction	6	0.047	0.74	0.6231
Error	33	0.064		

Table 1. (cont.)

Stream effects only				
Stream	6	1.360	20.44	0.0001
Error	40	0.067		

Figure Captions

Figure 1.-Six possible relationships between fish biomass, qualitative stream effects and quantitative site-level variation: (a) both stream and site-level effects are significant (constant slope, different intercepts); (b) site-level effects only (slopes and intercepts equal); (c) stream effects only (slopes equal to zero, different intercepts); (d) stream*site interaction (unequal slopes and intercepts); (e) stream and site-level effects confounded (cannot separate stream and site effects); (f) no relationship with stream or site effects).

Figure 2.-Plot of Lahontan cutthroat trout biomass against wetted stream width (log scale). Compare to possible relationships in Fig. 1.

Figure 1.

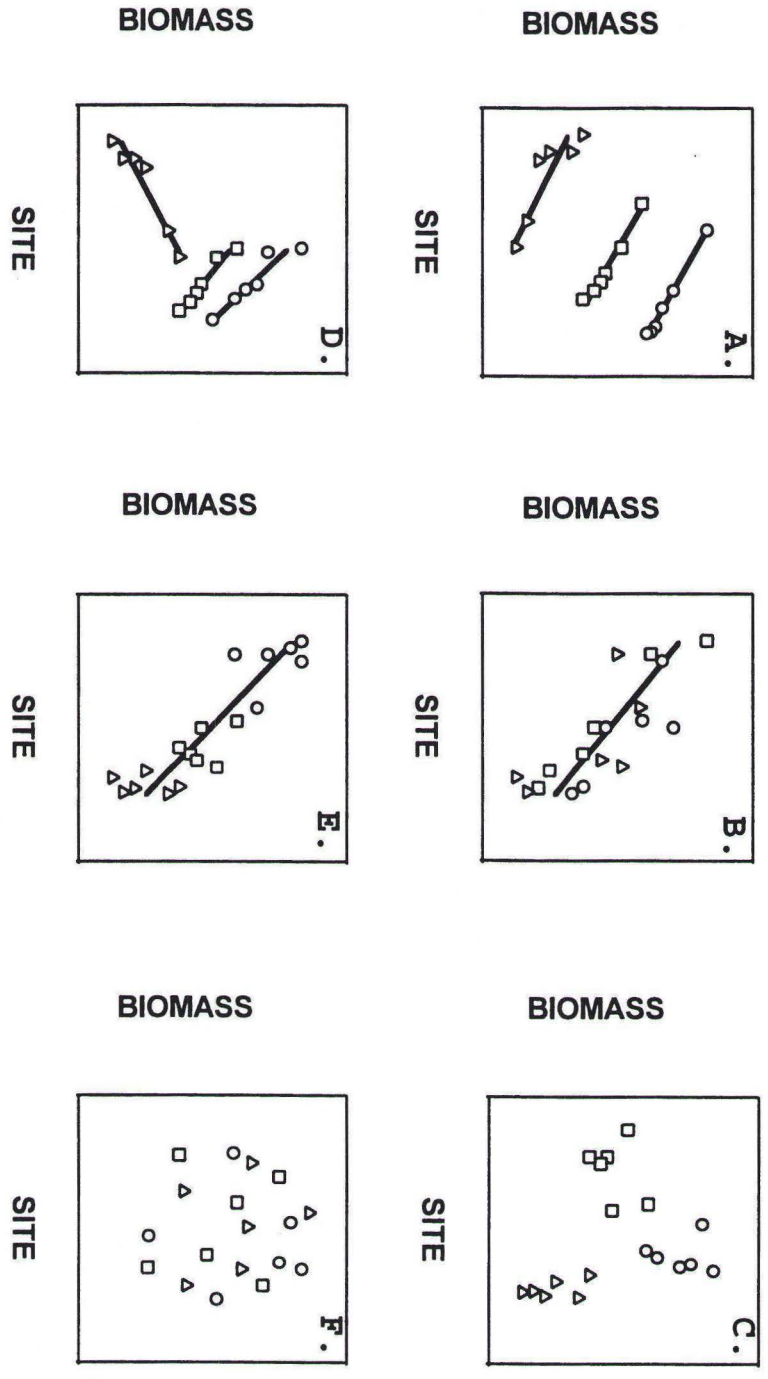
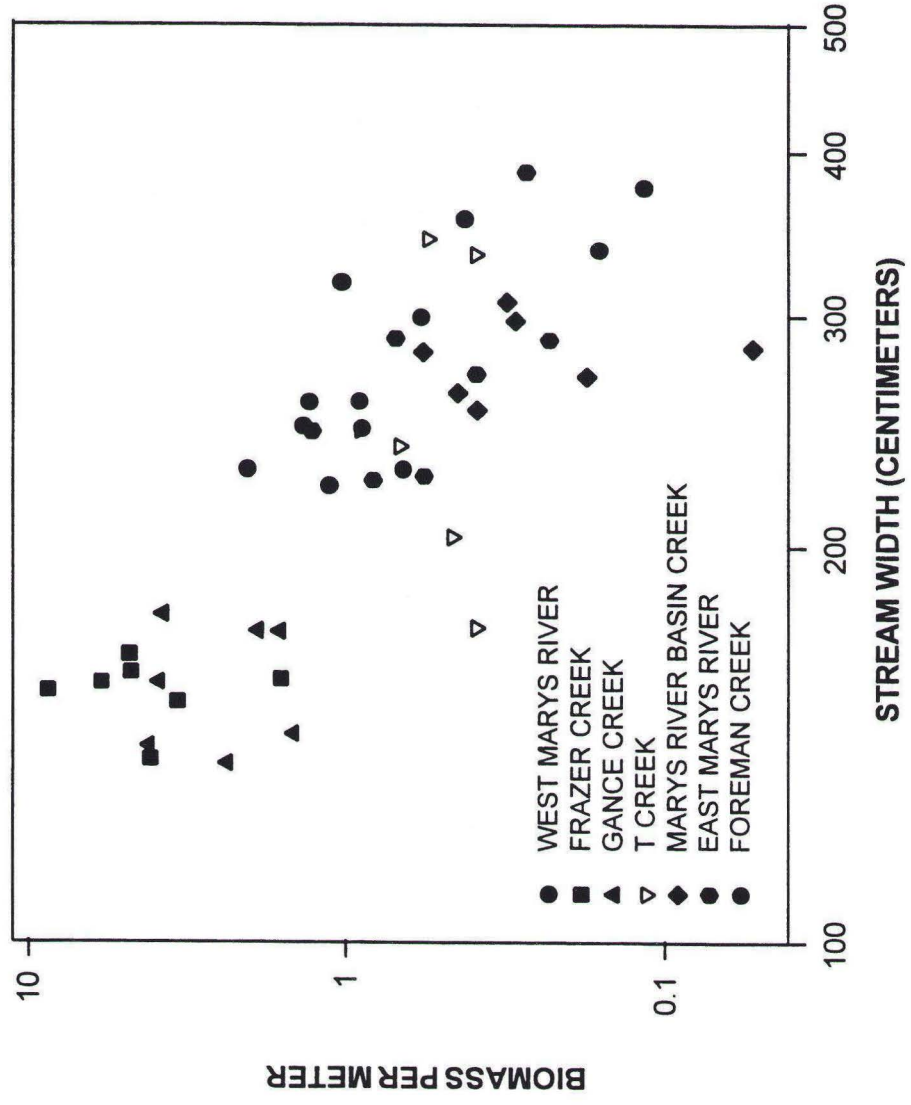

BIOMASS
SITE
A.
BIOMASS
SITE
B.
BIOMASS
SITE
C.
BIOMASS
SITE
D.
BIOMASS
SITE
E.
BIOMASS
SITE
F.

Figure 2.


BIOMASS PER METER
10
1
0.1
100
200
300
400
500
STREAM WIDTH (CENTIMETERS)
WEST MARYS RIVER
FRAZER CREEK
GANCE CREEK
T CREEK
MARYS RIVER BASIN CREEK
EAST MARYS RIVER
FOREMAN CREEK

Appendix 1. Lahontan cutthroat trout population data collected for seven streams in the upper Humboldt River basin, Nevada. Column headings are defined as follows:

TRANS M	Transect (site) length in meters.
TRANS M2	Transect (site) area in square meters.
TRANS M3	Transect (site) volume in cubic meters.
YOY POPEST	Removal estimate of young-of-year fish.
ADULT POPEST	Removal estimate of age 1+ fish.
TOTAL POPEST	Total fish population estimate.
YOY PER M, M2, M3	Young-of-year density expressed as linear, areal and volumetric quantities.
ADULT PER M, M2, M3	Adult density expressed as linear, areal and volumetric quantities.
TOTAL PER M, M2, M3	Total density expressed as linear, areal and volumetric quantities.
AVG YOY MASS	Average body mass (grams) of young-of-year fish.
AVG ADU MASS	Average body mass (grams) of age 1+ fish.
AVG TOT MASS	Average body mass of all fish.
TOT YOY MASS	Total mass of young-of-year fish.
TOT ADU MASS	Total mass of adult fish.
TOTAL MASS	Total mass of all fish.
GYOY PER M, M2 M3	Young-of-year mass expressed as linear, areal and volumetric quantities.
GADU PER M, M2, M3	Age 1+ fish mass expressed as linear, areal and volumetric quantities.
GTOT PER M, M2, M3	Total fish mass expressed as linear, areal and volumetric quantities.

Appendix 1. (cont.)

YEAR	STREAM	TRANSECT	TRANSM	TRANSM2	TRANSM3	YOY POPEST	ADULT POPEST
1993	EMR	1	26	84.68571	8.884571	0	0
1993	EMR	2	26	86.17143	10.11029	0	0
1993	EMR	3	25	70	9.178571	0	3
1993	EMR	4	25.5	133.3571	8.918857	0	1
1993	EMR	5	26	86.91429	9.768571	0	1
1993	EMR	6	26	73.91429	11.42514	0	0
1993	EMR	7	24	68.67692	7.513846	0	3
1993	FC	1	25	45.38462	2.980769	0	0
1993	FC	2	26	42.71429	3.932337	1	6
1993	FC	3	26	36.02857	3.844286	30	7
1993	FC	4	22	48.03333	8.582206	34	10
1993	FC	5	30	57.17647	5.096164	24	7
1993	FC	6	24	52.8	6.648366	51	5
1993	FC	7	26	50.88571	2.440286	125	12
1993	FNC	1	30	87	7.919762	0	8
1993	FNC	2	25	61.42857	4.689286	0	13
1993	FNC	3	25	52.85714	4.516552	0	15
1993	FNC	4	24	59.44615	3.600208	0	6
1993	FNC	5	26	62.4	6.176479	0	16
1993	FNC	6	29	74.675	6.119	0	14
1993	FNC	7	25	65	4.7125	0	12
1993	GC	1	26	49.77143	3.023429	4	0
1993	GC	2	26	44.2	2.863714	1	0
1993	GC	3	26	53.73333	5.019733	8	2
1993	GC	4	24	40.61538	3.485538	20	1
1993	GC	5	25	48.21429	3.3	39	1
1993	GC	6	32	50.07059	4.468706	6	2
1993	GC	7	25	42.85714	3.342857	11	1
1993	MRBC	1	25	90.35714	10.10714	0	1
1993	MRBC	2	26	71.31429	8.954722	0	1
1993	MRBC	3	25	76.07143	9.35	0	0
1993	MRBC	4	26	89.51429	8.649318	0	1
1993	MRBC	5	25	66.07143	5.460173	0	1
1993	MRBC	6	26	89.14286	6.358857	0	2
1993	MRBC	7	0	0	0	0	0
1993	WMR	1	25	94.64286	10.31109	0	2
1993	WMR	2	25	71.92308	8.808797	0	1
1993	WMR	3	25	81.42857	9.885714	0	6
1993	WMR	4	25	98.21429	10.49643	0	2
1993	WMR	5	25	98.92857	12.78214	0	2
1993	WMR	6	25	91.78571	9.010714	0	3
1993	WMR	7	25	63.21429	5.582143	0	3

Appendix 1. (cont.)

YEAR	STREAM	TRANSECT	TOTAL POPEST	YOY PER M	ADU PER M	TOT PER M	YOY PER M2
1993	EMR	1	0	0	0	0	0
1993	EMR	2	0	0	0	0	0
1993	EMR	3	3	0	0.12	0.12	0
1993	EMR	4	1	0	0.039216	0.039216	0
1993	EMR	5	1	0	0.038462	0.038462	0
1993	EMR	6	0	0	0	0	0
1993	EMR	7	3	0	0.125	0.125	0
1993	FC	1	0	0	0	0	0
1993	FC	2	7	0.038462	0.230769	0.269231	0.023411
1993	FC	3	37	1.153846	0.269231	1.423077	0.832672
1993	FC	4	44	1.545455	0.454545	2	0.707842
1993	FC	5	31	0.8	0.233333	1.033333	0.419753
1993	FC	6	56	2.125	0.208333	2.333333	0.965909
1993	FC	7	137	4.807692	0.461538	5.269231	2.456485
1993	FNC	1	8	0	0.266667	0.266667	0
1993	FNC	2	13	0	0.52	0.52	0
1993	FNC	3	15	0	0.6	0.6	0
1993	FNC	4	6	0	0.25	0.25	0
1993	FNC	5	16	0	0.615385	0.615385	0
1993	FNC	6	14	0	0.482759	0.482759	0
1993	FNC	7	12	0	0.48	0.48	0
1993	GC	1	4	0.153846	0	0.153846	0.080367
1993	GC	2	1	0.038462	0	0.038462	0.022624
1993	GC	3	10	0.307692	0.076923	0.384615	0.148883
1993	GC	4	21	0.833333	0.041667	0.875	0.492424
1993	GC	5	40	1.56	0.04	1.6	0.808889
1993	GC	6	8	0.1875	0.0625	0.25	0.119831
1993	GC	7	12	0.44	0.04	0.48	0.256667
1993	MRBC	1	1	0	0.04	0.04	0
1993	MRBC	2	1	0	0.038462	0.038462	0
1993	MRBC	3	0	0	0	0	0
1993	MRBC	4	1	0	0.038462	0.038462	0
1993	MRBC	5	1	0	0.04	0.04	0
1993	MRBC	6	2	0	0.076923	0.076923	0
1993	MRBC	7	0	0	0	0	0
1993	WMR	1	2	0	0.08	0.08	0
1993	WMR	2	1	0	0.04	0.04	0
1993	WMR	3	6	0	0.24	0.24	0
1993	WMR	4	2	0	0.08	0.08	0
1993	WMR	5	2	0	0.08	0.08	0
1993	WMR	6	3	0	0.12	0.12	0
1993	WMR	7	3	0	0.12	0.12	0

Appendix 1. (cont.)

YEAR	STREAM	TRANSECT	ADU PER M2	TOT PER M2	YOY PER M3	ADU PER M3	TOT PER M3
1993	EMR	1	0	0	0	0	0
1993	EMR	2	0	0	0	0	0
1993	EMR	3	0.042857	0.042857	0	0.326848	0.326848
1993	EMR	4	0.007499	0.007499	0	0.112122	0.112122
1993	EMR	5	0.011506	0.011506	0	0.102369	0.102369
1993	EMR	6	0	0	0	0	0
1993	EMR	7	0.043683	0.043683	0	0.399263	0.399263
1993	FC	1	0	0	0	0	0
1993	FC	2	0.140468	0.16388	0.254302	1.52581	1.780112
1993	FC	3	0.19429	1.026963	7.80379	1.820884	9.624675
1993	FC	4	0.208189	0.916031	3.961686	1.165202	5.126887
1993	FC	5	0.122428	0.542181	4.709425	1.373582	6.083007
1993	FC	6	0.094697	1.060606	7.671057	0.752064	8.423122
1993	FC	7	0.235823	2.692308	51.22351	4.917457	56.14097
1993	FNC	1	0.091954	0.091954	0	1.010131	1.010131
1993	FNC	2	0.211628	0.211628	0	2.772277	2.772277
1993	FNC	3	0.283784	0.283784	0	3.321118	3.321118
1993	FNC	4	0.100932	0.100932	0	1.666571	1.666571
1993	FNC	5	0.25641	0.25641	0	2.590473	2.590473
1993	FNC	6	0.187479	0.187479	0	2.287956	2.287956
1993	FNC	7	0.184615	0.184615	0	2.546419	2.546419
1993	GC	1	0	0.080367	1.323001	0	1.323001
1993	GC	2	0	0.022624	0.349197	0	0.349197
1993	GC	3	0.037221	0.186104	1.59371	0.398428	1.992138
1993	GC	4	0.024621	0.517045	5.737994	0.2869	6.024894
1993	GC	5	0.020741	0.82963	11.81818	0.30303	12.12121
1993	GC	6	0.039944	0.159774	1.342671	0.447557	1.790227
1993	GC	7	0.023333	0.28	3.290598	0.299145	3.589744
1993	MRBC	1	0.011067	0.011067	0	0.09894	0.09894
1993	MRBC	2	0.014022	0.014022	0	0.111673	0.111673
1993	MRBC	3	0	0	0	0	0
1993	MRBC	4	0.011171	0.011171	0	0.115616	0.115616
1993	MRBC	5	0.015135	0.015135	0	0.183144	0.183144
1993	MRBC	6	0.022436	0.022436	0	0.314522	0.314522
1993	MRBC	7	0	0	0	0	0
1993	WMR	1	0.021132	0.021132	0	0.193966	0.193966
1993	WMR	2	0.013904	0.013904	0	0.113523	0.113523
1993	WMR	3	0.073684	0.073684	0	0.606936	0.606936
1993	WMR	4	0.020364	0.020364	0	0.190541	0.190541
1993	WMR	5	0.020217	0.020217	0	0.156468	0.156468
1993	WMR	6	0.032685	0.032685	0	0.332937	0.332937
1993	WMR	7	0.047458	0.047458	0	0.537428	0.537428

Appendix 1. (cont.)

YEAR	STREAM	TRANSECT	AVG YOY MASS	AVG ADU MASS	TOT YOY MASS	TOT ADU MASS	TOTAL MASS
1993	EMR	1	0	0	0	0	0
1993	EMR	2	0	0	0	0	0
1993	EMR	3	0	28.16667	0	84.5	84.5
1993	EMR	4	0	7.6	0	7.6	7.6
1993	EMR	5	0	17	0	17	17
1993	EMR	6	0	0	0	0	0
1993	EMR	7	0	19.16667	0	57.5	57.5
1993	FC	1	0	0	0	0	0
1993	FC	2	1.1	27.2	1.1	163.2	164.3
1993	FC	3	1.207143	33.35714	36.21429	233.5	269.7143
1993	FC	4	0.993333	37.2	33.77333	372	405.7733
1993	FC	5	0.881818	38.32857	21.16364	268.3	289.4636
1993	FC	6	0.797826	52.28	40.68913	261.4	302.0891
1993	FC	7	1.31875	34.65833	164.8438	415.9	580.7438
1993	FNC	1	0	47.2125	0	377.7	377.7
1993	FNC	2	0.5	30.11818	0	391.5364	391.5364
1993	FNC	3	0.5	19.83077	0	297.4615	297.4615
1993	FNC	4	0	23.6	0	141.6	141.6
1993	FNC	5	0	37.20625	0	595.3	595.3
1993	FNC	6	0	30.8	0	431.2	431.2
1993	FNC	7	0	56.68333	0	680.2	680.2
1993	GC	1	0.75	0	3	0	3
1993	GC	2	0.5	0	0.5	0	0.5
1993	GC	3	0.685714	102.4	5.485712	204.8	210.2857
1993	GC	4	0.957895	49.6	19.15789	49.6	68.75789
1993	GC	5	0.720513	45.3	28.1	45.3	73.4
1993	GC	6	1.916667	61.45	11.5	122.9	134.4
1993	GC	7	1.791667	131.7	19.70833	131.7	151.4083
1993	MRBC	1	0	4.8	0	4.8	4.8
1993	MRBC	2	0	15.8	0	15.8	15.8
1993	MRBC	3	0	0	0	0	0
1993	MRBC	4	0	36.8	0	36.8	36.8
1993	MRBC	5	0	15	0	15	15
1993	MRBC	6	0	12.6	0	25.2	25.2
1993	MRBC	7	0	0	0	0	0
1993	WMR	1	0	11.45	0	22.9	22.9
1993	WMR	2	0	6	0	6	6
1993	WMR	3	0	25.48333	0	152.9	152.9
1993	WMR	4	0	8.7	0	17.4	17.4
1993	WMR	5	0	72.6	0	145.2	145.2
1993	WMR	6	0	44	0	132	132
1993	WMR	7	0	15	0	45	45

Appendix 1. (cont.)

YEAR	STREAM	TRANSECT	GYOY PER M	GADU PER M	GTOT PER M	GYOY PER M2	GADU PER M2
1993	EMR	1					
1993	EMR	2	0	0	0	0	0
1993	EMR	3	0	0	0	0	0
1993	EMR	4	0	3.38	3.38	0	1.207143
1993	EMR	5	0	0.298039	0.298039	0	0.05699
1993	EMR	6	0	0.653846	0.653846	0	0.195595
1993	EMR	7	0	0	0	0	0
1993	FC	1	0	2.395833	2.395833	0	0.837254
1993	FC	2	0	0	0	0	0
1993	FC	3	0.042308	6.276923	6.276923	0.025753	3.820736
1993	FC	4	1.392857	8.980769	8.980769	1.005155	6.480967
1993	FC	5	1.535152	16.90909	16.90909	0.703123	7.744622
1993	FC	6	0.705455	8.943333	8.943333	0.370146	4.69249
1993	FC	7	1.69538	10.89167	10.89167	0.770627	4.950758
1993	FNC	1	6.340144	15.99615	15.99615	3.23949	8.173217
1993	FNC	2	0	12.59	12.59	0	4.341379
1993	FNC	3	0	15.66145	15.66145	0	6.373848
1993	FNC	4	0	11.89846	11.89846	0	5.627651
1993	FNC	5	0	5.9	5.9	0	2.381988
1993	FNC	6	0	22.89615	22.89615	0	9.540064
1993	FNC	7	0	14.86897	14.86897	0	5.774356
1993	GC	1	0	27.208	27.208	0	10.46462
1993	GC	2	0.115385	0	0	0.060276	0
1993	GC	3	0.019231	0	0	0.011312	0
1993	GC	4	0.210989	7.876923	7.876923	0.102091	3.811414
1993	GC	5	0.798246	2.066667	2.066667	0.471691	1.221212
1993	GC	6	1.124	1.812	1.812	0.582815	0.939556
1993	GC	7	0.359375	3.840625	3.840625	0.229676	2.454535
1993	MRBC	1	0.788333	5.268	5.268	0.459861	3.073
1993	MRBC	2	0	0.192	0.192	0	0.053123
1993	MRBC	3	0	0.607692	0.607692	0	0.221554
1993	MRBC	4	0	0	0	0	0
1993	MRBC	5	0	1.415385	1.415385	0	0.411108
1993	MRBC	6	0	0.6	0.6	0	0.227027
1993	MRBC	7	0	0.969231	0.969231	0	0.282692
1993	WMR	1	0	0	0	0	0
1993	WMR	2	0	0.916	0.916	0	0.241962
1993	WMR	3	0	0.24	0.24	0	0.083422
1993	WMR	4	0	6.116	6.116	0	1.877719
1993	WMR	5	0	0.696	0.696	0	0.177164
1993	WMR	6	0	5.808	5.808	0	1.467726
1993	WMR	7	0	5.28	5.28	0	1.438132
			0	1.8	1.8	0	0.711864

Appendix 1. (cont.)

YEAR	STREAM	TRANSECT	GTOT PER M2	GYOY PER M3	GADU PER M3	GTOT PER M3
1993	EMR	1	0	0	0	0
1993	EMR	2	0	0	0	0
1993	EMR	3	1.207143	0	9.206226	9.206226
1993	EMR	4	0.05699	0	0.852127	0.852127
1993	EMR	5	0.195595	0	1.740275	1.740275
1993	EMR	6	0	0	0	0
1993	EMR	7	0.837254	0	7.652539	7.652539
1993	FC	1	0	0	0	0
1993	FC	2	3.846488	0.279732	41.50204	41.78177
1993	FC	3	7.486122	9.42029	60.7395	70.15979
1993	FC	4	8.447745	3.935274	43.3455	47.28077
1993	FC	5	5.062636	4.152856	52.64745	56.8003
1993	FC	6	5.721385	6.12017	39.31793	45.4381
1993	FC	7	11.41271	67.551	170.4309	237.9819
1993	FNC	1	4.341379	0	47.69083	47.69083
1993	FNC	2	6.373848	0	83.49595	83.49595
1993	FNC	3	5.627651	0	65.86032	65.86032
1993	FNC	4	2.381988	0	39.33106	39.33106
1993	FNC	5	9.540064	0	96.38177	96.38177
1993	FNC	6	5.774356	0	70.46903	70.46903
1993	FNC	7	10.46462	0	144.3395	144.3395
1993	GC	1	0.060276	0.992251	0	0.992251
1993	GC	2	0.011312	0.174598	0	0.174598
1993	GC	3	3.913506	1.092829	40.79898	41.89181
1993	GC	4	1.692903	5.496395	14.23023	19.72662
1993	GC	5	1.52237	8.515152	13.72727	22.24242
1993	GC	6	2.684211	2.573452	27.50237	30.07582
1993	GC	7	3.532861	5.895655	39.39744	45.29309
1993	MRBC	1	0.053123	0	0.474912	0.474912
1993	MRBC	2	0.221554	0	1.764432	1.764432
1993	MRBC	3	0	0	0	0
1993	MRBC	4	0.411108	0	4.254671	4.254671
1993	MRBC	5	0.227027	0	2.747166	2.747166
1993	MRBC	6	0.282692	0	3.962976	3.962976
1993	MRBC	7	0	0	0	0
1993	WMR	1	0.241962	0	2.22091	2.22091
1993	WMR	2	0.083422	0	0.681137	0.681137
1993	WMR	3	1.877719	0	15.46676	15.46676
1993	WMR	4	0.177164	0	1.657707	1.657707
1993	WMR	5	1.467726	0	11.3596	11.3596
1993	WMR	6	1.438132	0	14.64923	14.64923
1993	WMR	7	0.711864	0	8.06142	8.06142

Appendix 1. (cont.)

YEAR	STREAM	TRANSECT	TRANSM	TRANSM2	TRANSM3	YOY POPEST	ADULT POPEST
1994	EMR	1	26	63.94143	3.509166	4	1
1994	EMR	2	30	66.80625	4.516381	36	1
1994	EMR	3	24	44.41846	3.76418	9	4
1994	EMR	4	28	48.68267	2.737048	11	1
1994	EMR	5	26	59.48429	6.167954	101	4
1994	EMR	6	26	44.59	4.198892	116	2
1994	EMR	7	20	42.10909	2.788132	72	6
1994	FC	1	24	17.26154	0.814391	0	0
1994	FC	2	24	28.72615	3.03466	0	7
1994	FC	3	24	26.64	2.482302	12	39
1994	FC	4	26	42.45429	7.126255	20	46
1994	FC	5	22	32.04667	2.950964	18	41
1994	FC	6	24	30.33231	3.087673	0	13
1994	FC	7	28	49.69067	3.748885	14	62
1994	FNC	1	24	55.27385	5.066769	0	7
1994	FNC	2	28	59.71467	5.526924	0	16
1994	FNC	3	26	51.94429	5.138774	0	23
1994	FNC	4	26	54.93429	3.83232	0	10
1994	FNC	5	32	80.54588	9.831336	0	12
1994	FNC	6	26	63.81143	6.464705	0	13
1994	FNC	7	24	54.24	5.841231	0	11
1994	GC	1	26	43.21571	3.585875	9	5
1994	GC	2	26	39.05571	3.10121	24	3
1994	GC	3	28	43.88533	4.047203	26	26
1994	GC	4	20	30.36364	2.373884	15	7
1994	GC	5	24	45.28615	3.843517	39	9
1994	GC	6	24	30.97846	3.296426	29	11
1994	GC	7	24	38.27077	3.547406	37	7
1994	MRBC	1	26	47.59857	4.459533	41	5
1994	MRBC	2	26	53.70857	5.75449	78	21
1994	MRBC	3	24	40.15385	3.428521	1	12
1994	MRBC	4	26	50.29143	3.292891	35	15
1994	MRBC	5	28	59.248	5.12166	28	7
1994	MRBC	6	28	44.81867	1.802706	25	15
1994	MRBC	7	24	50.30769	4.166509	0	0
1994	WMR	1	24	85.34769	2.305824	0	4
1994	WMR	2	20	43.72727	1.880916	0	3
1994	WMR	3	20	54.81818	2.063418	0	3
1994	WMR	4	24	90.46154	2.318141	0	5
1994	WMR	5	26	83.31143	4.216148	0	8
1994	WMR	6	28	76.45867	3.4632	0	6
1994	WMR	7	24	72.36923	1.834235	0	2
1994	T	1	26	33.46571	10.58548	0	2
1994	T	2	28	39.368	7.69865	0	7
1994	T	3	26	44.18143	7.428694	0	7
1994	T	4	26	34.41286	8.744615	0	21
1994	T	5	28	50.512	11.47134	2	24
1994	T	6	26	40.56	6.807855	27	5
1994	T	7	20	27.56364	4.608126	54	9

Appendix 1. (cont.)

YEAR	STREAM	TRANSECT	TOTAL POPEST	YOY PER M	ADU PER M	TOT PER M	YOY PER M2
1994	EMR	1	5	0.153846	0.038462	0.192308	0.062557
1994	EMR	2	37	1.2	0.033333	1.233333	0.538872
1994	EMR	3	13	0.375	0.166667	0.541667	0.202618
1994	EMR	4	12	0.392857	0.035714	0.428571	0.225953
1994	EMR	5	105	3.884615	0.153846	4.038462	1.697927
1994	EMR	6	118	4.461538	0.076923	4.538462	2.60148
1994	EMR	7	78	3.6	0.3	3.9	1.709845
1994	FC	1	0	0	0	0	0
1994	FC	2	7	0	0.291667	0.291667	0
1994	FC	3	51	0.5	1.625	2.125	0.45045
1994	FC	4	66	0.769231	1.769231	2.538462	0.471095
1994	FC	5	59	0.818182	1.863636	2.681818	0.561681
1994	FC	6	13	0	0.541667	0.541667	0
1994	FC	7	76	0.5	2.214286	2.714286	0.281743
1994	FNC	1	7	0	0.291667	0.291667	0
1994	FNC	2	16	0	0.571429	0.571429	0
1994	FNC	3	23	0	0.884615	0.884615	0
1994	FNC	4	10	0	0.384615	0.384615	0
1994	FNC	5	12	0	0.375	0.375	0
1994	FNC	6	13	0	0.5	0.5	0
1994	FNC	7	11	0	0.458333	0.458333	0
1994	GC	1	14	0.346154	0.192308	0.538462	0.208258
1994	GC	2	27	0.923077	0.115385	1.038462	0.614507
1994	GC	3	52	0.928571	0.928571	1.857143	0.592453
1994	GC	4	22	0.75	0.35	1.1	0.494012
1994	GC	5	48	1.625	0.375	2	0.86119
1994	GC	6	40	1.208333	0.458333	1.666667	0.936134
1994	GC	7	44	1.541667	0.291667	1.833333	0.966795
1994	MRBC	1	46	1.576923	0.192308	1.769231	0.86137
1994	MRBC	2	99	3	0.807692	3.807692	1.452282
1994	MRBC	3	13	0.041667	0.5	0.541667	0.024904
1994	MRBC	4	50	1.346154	0.576923	1.923077	0.695944
1994	MRBC	5	35	1	0.25	1.25	0.47259
1994	MRBC	6	40	0.892857	0.535714	1.428571	0.557803
1994	MRBC	7	0	0	0	0	0
1994	WMR	1	4	0	0.166667	0.166667	0
1994	WMR	2	3	0	0.15	0.15	0
1994	WMR	3	3	0	0.15	0.15	0
1994	WMR	4	5	0	0.208333	0.208333	0
1994	WMR	5	8	0	0.307692	0.307692	0
1994	WMR	6	6	0	0.214286	0.214286	0
1994	WMR	7	2	0	0.083333	0.083333	0
1994	T	1	2	0	0.076923	0.076923	0
1994	T	2	7	0	0.25	0.25	0
1994	T	3	7	0	0.269231	0.269231	0
1994	T	4	21	0	0.807692	0.807692	0
1994	T	5	26	0.071429	0.857143	0.928571	0.039595
1994	T	6	32	1.038462	0.192308	1.230769	0.66568
1994	T	7	63	2.7	0.45	3.15	1.959103

Appendix 1. (cont.)

YEAR	STREAM	TRANSECT	TOT PER M2	YOY PER M3	ADU PER M3	TOT PER M3	AVG YOY MASS
1994	EMR	1	0.078197	1.139872	0.284968	1.42484	0.425
1994	EMR	2	0.55384	7.970984	0.221416	8.1924	0.552778
1994	EMR	3	0.292671	2.390959	1.062648	3.453608	0.522222
1994	EMR	4	0.246494	4.018929	0.365357	4.384286	0.472727
1994	EMR	5	1.765172	16.37496	0.648513	17.02347	0.453933
1994	EMR	6	2.646333	27.62634	0.476316	28.10265	0.745283
1994	EMR	7	1.852332	25.82374	2.151978	27.97572	0.861905
1994	FC	1	0	0	0	0	0
1994	FC	2	0.24368	0	2.306683	2.306683	0
1994	FC	3	1.914414	4.834223	15.71123	20.54545	0.433333
1994	FC	4	1.554613	2.806523	6.455003	9.261526	0.49
1994	FC	5	1.841065	6.099702	13.89377	19.99347	0.731579
1994	FC	6	0.428586	0	4.21029	4.21029	0
1994	FC	7	1.529462	3.734444	16.53825	20.2727	0.707143
1994	FNC	1	0.126642	0	1.381551	1.381551	0
1994	FNC	2	0.267941	0	2.894919	2.894919	0
1994	FNC	3	0.442782	0	4.475776	4.475776	0
1994	FNC	4	0.182036	0	2.609385	2.609385	0
1994	FNC	5	0.148983	0	1.220587	1.220587	0
1994	FNC	6	0.203725	0	2.010919	2.010919	0
1994	FNC	7	0.202802	0	1.883165	1.883165	0
1994	GC	1	0.323956	2.509847	1.39436	3.904207	0.6
1994	GC	2	0.69132	7.738916	0.967364	8.70628	1.028571
1994	GC	3	1.184906	6.42419	6.42419	12.84838	0.718182
1994	GC	4	0.724551	6.318758	2.948754	9.267511	0.65
1994	GC	5	1.059927	10.14696	2.341605	12.48856	0.667568
1994	GC	6	1.29122	8.797407	3.336947	12.13435	0.841667
1994	GC	7	1.149703	10.43016	1.973273	12.40343	0.651429
1994	MRBC	1	0.966416	9.193788	1.121194	10.31498	0.053659
1994	MRBC	2	1.843281	13.55463	3.649324	17.20396	0.565278
1994	MRBC	3	0.323755	0.291671	3.500052	3.791723	0.2
1994	MRBC	4	0.994205	10.62896	4.555267	15.18422	0.408571
1994	MRBC	5	0.590737	5.466977	1.366744	6.833721	0.606667
1994	MRBC	6	0.892485	13.86804	8.320823	22.18886	0.170833
1994	MRBC	7	0	0	0	0	0
1994	WMR	1	0.046867	0	1.734737	1.734737	0
1994	WMR	2	0.068607	0	1.594968	1.594968	0
1994	WMR	3	0.054726	0	1.453898	1.453898	0
1994	WMR	4	0.055272	0	2.156901	2.156901	0
1994	WMR	5	0.096025	0	1.897466	1.897466	0
1994	WMR	6	0.078474	0	1.732502	1.732502	0
1994	WMR	7	0.027636	0	1.090373	1.090373	0
1994	T	1	0.059763	0	0.188938	0.188938	0
1994	T	2	0.177809	0	0.90925	0.90925	0
1994	T	3	0.158438	0	0.942292	0.942292	0
1994	T	4	0.610237	0	2.401478	2.401478	0
1994	T	5	0.514729	0.174348	2.09217	2.266518	0.7
1994	T	6	0.788955	3.966007	0.734446	4.700452	0.755556
1994	T	7	2.28562	11.71843	1.953071	13.6715	0.724444

Appendix 1. (cont.)

YEAR	STREAM	TRANSECT	AVG ADU MASS	TOT YOY MASS	TOT ADU MASS	TOTAL MASS	GYOY PER M
1994	EMR	1	12.2	1.7	12.2	13.9	0.065385
1994	EMR	2	11.5	19.90001	11.5	31.40001	0.663334
1994	EMR	3	8.675	4.699998	34.7	39.4	0.195833
1994	EMR	4	12.3	5.199997	12.3	17.5	0.185714
1994	EMR	5	8.9	45.84723	35.6	81.44723	1.763355
1994	EMR	6	7.95	86.45283	15.9	102.3528	3.325109
1994	EMR	7	8.666667	62.05716	52	114.0572	3.102858
1994	FC	1	0	0	0	0	0
1994	FC	2	18.64286	0	130.5	130.5	0
1994	FC	3	13.29231	5.199996	518.4001	523.6001	0.216667
1994	FC	4	17.13864	9.8	788.3774	798.1774	0.376923
1994	FC	5	11.84634	13.16842	485.6999	498.8684	0.598565
1994	FC	6	17.1	0	222.3	222.3	0
1994	FC	7	12.41935	9.900002	769.9997	779.8997	0.353572
1994	FNC	1	35.41429	0	247.9	247.9	0
1994	FNC	2	27.175	0	434.8	434.8	0
1994	FNC	3	22.76087	0	523.5	523.5	0
1994	FNC	4	32.65	0	326.5	326.5	0
1994	FNC	5	61.09167	0	733.1	733.1	0
1994	FNC	6	43.78333	0	569.1833	569.1833	0
1994	FNC	7	54.62727	0	600.9	600.9	0
1994	GC	1	37.42	5.4	187.1	192.5	0.207692
1994	GC	2	17.66667	24.6857	53.00001	77.68571	0.94945
1994	GC	3	15.38077	18.67273	399.9	418.5728	0.666883
1994	GC	4	14.18571	9.75	99.29997	109.05	0.4875
1994	GC	5	16.12222	26.03515	145.1	171.1351	1.084798
1994	GC	6	19.1	24.40834	210.1	234.5083	1.017014
1994	GC	7	19.11429	24.10287	133.8	157.9029	1.004286
1994	MRBC	1	8.88	2.199999	44.4	46.6	0.084615
1994	MRBC	2	9.085714	44.09168	190.8	234.8917	1.695834
1994	MRBC	3	8.991667	0.2	107.9	108.1	0.008333
1994	MRBC	4	7.38	14.29999	110.7	125	0.549999
1994	MRBC	5	9.828571	16.98668	68.8	85.78667	0.606667
1994	MRBC	6	6.085714	4.270825	91.28571	95.55654	0.152529
1994	MRBC	7	0	0	0	0	0
1994	WMR	1	22.2	0	88.8	88.8	0
1994	WMR	2	9.866667	0	29.6	29.6	0
1994	WMR	3	8.43333	0	25.29999	25.29999	0
1994	WMR	4	16.78	0	83.9	83.9	0
1994	WMR	5	16.85	0	134.8	134.8	0
1994	WMR	6	12.36667	0	74.20002	74.20002	0
1994	WMR	7	20.65	0	41.3	41.3	0
1994	T	1	30.7	0	61.4	61.4	0
1994	T	2	11.7	0	81.9	81.9	0
1994	T	3	14.8375	0	103.8625	103.8625	0
1994	T	4	9.119048	0	191.5	191.5	0
1994	T	5	15.0913	1.4	362.1912	363.5912	0.05
1994	T	6	12.68	20.40001	63.4	83.80001	0.784616
1994	T	7	6.766667	39.11998	60.9	100.02	1.955999

Appendix 1. (cont.)

YEAR	STREAM	TRANSECT	GADU PER M	GTOT PER M	GYOY PER M2	GADU PER M2	GTOT PER M2
1994	EMR	1	0.469231	0.534615	0.026587	0.1908	0.217386
1994	EMR	2	0.383333	1.046667	0.297876	0.17214	0.470016
1994	EMR	3	1.445833	1.641667	0.105812	0.781207	0.887019
1994	EMR	4	0.439286	0.625	0.106814	0.252657	0.359471
1994	EMR	5	1.369231	3.132586	0.770745	0.598477	1.369223
1994	EMR	6	0.611538	3.936647	1.938839	0.356582	2.295421
1994	EMR	7	2.6	5.702858	1.473724	1.234888	2.708611
1994	FC	1	0	0	0	0	0
1994	FC	2	5.437501	5.437501	0	4.542899	4.542899
1994	FC	3	21.6	21.81667	0.195195	19.45946	19.65466
1994	FC	4	30.32221	30.69913	0.230837	18.57003	18.80087
1994	FC	5	22.07727	22.67583	0.410914	15.15602	15.56693
1994	FC	6	9.2625	9.2625	0	7.328819	7.328819
1994	FC	7	27.49999	27.85356	0.199233	15.49586	15.69509
1994	FNC	1	10.32917	10.32917	0	4.484943	4.484943
1994	FNC	2	15.52857	15.52857	0	7.281293	7.281293
1994	FNC	3	20.13462	20.13462	0	10.07811	10.07811
1994	FNC	4	12.55769	12.55769	0	5.943465	5.943465
1994	FNC	5	22.90938	22.90938	0	9.101645	9.101645
1994	FNC	6	21.89167	21.89167	0	8.919771	8.919771
1994	FNC	7	25.0375	25.0375	0	11.07854	11.07854
1994	GC	1	7.196154	7.403846	0.124955	4.329444	4.454398
1994	GC	2	2.038462	2.987912	0.632064	1.357036	1.9891
1994	GC	3	14.28214	14.94903	0.425489	9.112384	9.537873
1994	GC	4	4.964999	5.452499	0.321108	3.270358	3.591400
1994	GC	5	6.045833	7.130631	0.574903	3.204069	3.778973
1994	GC	6	8.754167	9.771181	0.787913	6.782132	7.570045
1994	GC	7	5.575001	6.579288	0.629798	3.496142	4.12594
1994	MRBC	1	1.707692	1.792308	0.04622	0.932801	0.979021
1994	MRBC	2	7.338461	9.034295	0.820943	3.552505	4.373449
1994	MRBC	3	4.495834	4.504167	0.004981	2.687165	2.692146
1994	MRBC	4	4.257692	4.807692	0.284342	2.20117	2.485513
1994	MRBC	5	2.457143	3.06381	0.286705	1.161221	1.447925
1994	MRBC	6	3.260204	3.412733	0.095291	2.036779	2.13207
1994	MRBC	7	0	0	0	0	0
1994	WMR	1	3.7	3.7	0	1.04045	1.04045
1994	WMR	2	1.48	1.48	0	0.676923	0.676923
1994	WMR	3	1.265	1.265	0	0.461526	0.461526
1994	WMR	4	3.495833	3.495833	0	0.927466	0.927466
1994	WMR	5	5.184615	5.184615	0	1.618025	1.618025
1994	WMR	6	2.650001	2.650001	0	0.970459	0.970459
1994	WMR	7	1.720833	1.720833	0	0.570685	0.570685
1994	T	1	2.361538	2.361538	0	1.834714	1.834714
1994	T	2	2.925	2.925	0	2.08037	2.08037
1994	T	3	3.994712	3.994712	0	2.350818	2.350818
1994	T	4	7.365385	7.365385	0	5.564781	5.564781
1994	T	5	12.9354	12.9854	0.027716	7.170399	7.198115
1994	T	6	2.438462	3.223077	0.502959	1.563116	2.066075
1994	T	7	3.045	5.000999	1.41926	2.209433	3.628693

Appendix 1. (cont.)

YEAR	STREAM	TRANSECT	GYOY PER M2	GADU PER M2	GTOT PER M2	GYOY PER M3	GADU PER M3
1994	EMR	1	0.026587	0.1908	0.217386	0.484446	3.476609
1994	EMR	2	0.297876	0.17214	0.470016	4.406185	2.546287
1994	EMR	3	0.105812	0.781207	0.887019	1.248611	9.218475
1994	EMR	4	0.106814	0.252657	0.359471	1.899856	4.493893
1994	EMR	5	0.770745	0.598477	1.369223	7.433135	5.771768
1994	EMR	6	1.938839	0.356582	2.295421	20.58944	3.786714
1994	EMR	7	1.473724	1.234888	2.708611	22.25761	18.65048
1994	FC	1	0	0	0	0	0
1994	FC	2	0	4.542899	4.542899	0	43.00317
1994	FC	3	0.195195	19.45946	19.65466	2.094828	208.8385
1994	FC	4	0.230837	18.57003	18.80087	1.375196	110.63
1994	FC	5	0.410914	15.15602	15.56693	4.462414	164.5903
1994	FC	6	0	7.328819	7.328819	0	71.99596
1994	FC	7	0.199233	15.49586	15.69509	2.640786	205.3943
1994	FNC	1	0	4.484943	4.484943	0	48.92665
1994	FNC	2	0	7.281293	7.281293	0	78.66943
1994	FNC	3	0	10.07811	10.07811	0	101.8726
1994	FNC	4	0	5.943465	5.943465	0	85.19643
1994	FNC	5	0	9.101645	9.101645	0	74.5677
1994	FNC	6	0	8.919771	8.919771	0	88.04474
1994	FNC	7	0	11.07854	11.07854	0	102.8722
1994	GC	1	0.124955	4.329444	4.454398	1.505908	52.17694
1994	GC	2	0.632064	1.357036	1.9891	7.960024	17.09011
1994	GC	3	0.425489	9.112384	9.537873	4.613737	98.80899
1994	GC	4	0.321108	3.270358	3.591466	4.107193	41.83016
1994	GC	5	0.574903	3.204069	3.778973	6.773783	37.75188
1994	GC	6	0.787913	6.782132	7.570045	7.404487	63.73569
1994	GC	7	0.629798	3.496142	4.12594	6.794507	37.71771
1994	MRBC	1	0.04622	0.932801	0.979021	0.493325	9.9562
1994	MRBC	2	0.820943	3.552505	4.373449	7.662136	33.15672
1994	MRBC	3	0.004981	2.687165	2.692146	0.058334	31.4713
1994	MRBC	4	0.284342	2.20117	2.485513	4.342684	33.61787
1994	MRBC	5	0.286705	1.161221	1.447925	3.316635	13.43314
1994	MRBC	6	0.095291	2.036779	2.13207	2.369118	50.63815
1994	MRBC	7	0	0	0	0	0
1994	WMR	1	0	1.04045	1.04045	0	38.51117
1994	WMR	2	0	0.676923	0.676923	0	15.73702
1994	WMR	3	0	0.461526	0.461526	0	12.2612
1994	WMR	4	0	0.927466	0.927466	0	36.1928
1994	WMR	5	0	1.618025	1.618025	0	31.97231
1994	WMR	6	0	0.970459	0.970459	0	21.42528
1994	WMR	7	0	0.570685	0.570685	0	22.5162
1994	T	1	0	1.834714	1.834714	0	5.800396
1994	T	2	0	2.08037	2.08037	0	10.63823
1994	T	3	0	2.350818	2.350818	0	13.98126
1994	T	4	0	5.564781	5.564781	0	21.89919
1994	T	5	0.027716	7.170399	7.198115	0.122043	31.57357
1994	T	6	0.502959	1.563116	2.066075	2.99654	9.312771
1994	T	7	1.41926	2.209433	3.628693	8.489346	13.21578

Appendix 1. (cont.)

YEAR	STREAM	TRANSECT	GTOT PER M3
1994	EMR	1	3.961055
1994	EMR	2	6.952471
1994	EMR	3	10.46709
1994	EMR	4	6.393749
1994	EMR	5	13.2049
1994	EMR	6	24.37615
1994	EMR	7	40.90809
1994	FC	1	0
1994	FC	2	43.00317
1994	FC	3	210.9333
1994	FC	4	112.0052
1994	FC	5	169.0527
1994	FC	6	71.99596
1994	FC	7	208.0351
1994	FNC	1	48.92665
1994	FNC	2	78.66943
1994	FNC	3	101.8726
1994	FNC	4	85.19643
1994	FNC	5	74.5677
1994	FNC	6	88.04474
1994	FNC	7	102.8722
1994	GC	1	53.68285
1994	GC	2	25.05013
1994	GC	3	103.4227
1994	GC	4	45.93736
1994	GC	5	44.52566
1994	GC	6	71.14018
1994	GC	7	44.51222
1994	MRBC	1	10.44952
1994	MRBC	2	40.81885
1994	MRBC	3	31.52963
1994	MRBC	4	37.96056
1994	MRBC	5	16.74978
1994	MRBC	6	53.00727
1994	MRBC	7	0
1994	WMR	1	38.51117
1994	WMR	2	15.73702
1994	WMR	3	12.2612
1994	WMR	4	36.1928
1994	WMR	5	31.97231
1994	WMR	6	21.42528
1994	WMR	7	22.5162
1994	T	1	5.800396
1994	T	2	10.63823
1994	T	3	13.98126
1994	T	4	21.89919
1994	T	5	31.69561
1994	T	6	12.30931
1994	T	7	21.70513

Appendix 1. (cont.)

YEAR	STREAM	TRANSECT	TRANSM	TRANSM2	TRANSM3	YOYPOPEST	ADULTPOPEST
1995	EMR	1	24	69.01091	9.536053	0	4
1995	EMR	2	30	81.26	9.119178	0	4
1995	EMR	3	24	53.98	6.492594	0	5
1995	EMR	4	26	100.42	9.810262	0	2
1995	EMR	5	27	77.84308	12.03574	0	12
1995	EMR	6	26	58.88	8.469662	0	11
1995	EMR	7	20	49	4.834667	0	10
1995	FC	1	33	52.47	4.940925	0	7
1995	FC	2	29	46.66929	4.86694	0	17
1995	FC	3	28	38.64	4.7012	0	18
1995	FC	4	24	39.84	8.3332	8	34
1995	FC	5	24	37.9	4.569056	0	24
1995	FC	6	28	42.76	6.495448	1	18
1995	FC	7	27	42.05769	4.162633	11	31
1995	FNC	1	27	61.90269	7.53596	0	0
1995	FNC	2	30	68.8	8.424178	0	0
1995	FNC	3	25	64.47917	6.985243	1	15
1995	FNC	4	28	72.3	6.283214	0	0
1995	FNC	5	30	66.86	8.350071	0	0
1995	FNC	6	25	61.8125	7.589201	0	0
1995	FNC	7	25	61.5625	5.814236	0	0
1995	GC	1	25	43.22917	4.214844	3	5
1995	GC	2	25	36.08333	3.608333	3	4
1995	GC	3	31	55.18	6.915893	6	20
1995	GC	4	22	34.76	3.792	3	9
1995	GC	5	24	33.88	2.813922	3	11
1995	GC	6	26	35.6	3.943385	0	0
1995	GC	7	23	39.72727	4.153306	2	6
1995	MRBC	1	23	65.19455	9.403819	0	1
1995	MRBC	2	25	65.52083	11.70275	0	3
1995	MRBC	3	29	86.275	12.50988	0	4
1995	MRBC	4	27	83.07692	11.31124	0	4
1995	MRBC	5	30	80.93571	8.768036	0	4
1995	MRBC	6	24	61.01425	4.796398	0	3
1995	MRBC	7	26	73.18	10.32026	0	8
1995	WMR	1	23	77.53091	13.90858	0	2
1995	WMR	2	22	59.24	12.88919	0	0
1995	WMR	3	22	70.06	10.7213	0	4
1995	WMR	4	23	81.92182	11.17116	0	3
1995	WMR	5	25	94.04167	16.3528	0	2
1995	WMR	6	27	80.89615	11.26323	0	2
1995	WMR	7	25	62.10417	8.401314	0	11
1995	T	1	22	58.46	5.721994	0	0
1995	T	2	24	82.47273	8.722116	0	2
1995	T	3	32	106.9	10.97952	0	3
1995	T	4	28	48.64	5.338819	0	2
1995	T	5	34	81.1	9.445765	0	14
1995	T	6	28	68.66462	10.47576	0	12
1995	T	7	21	42.735	4.081193	0	3

Appendix 1. (cont.)

YEAR	STREAM	TRANSECT	TOTAL POPEST	YOY PER M	ADU PER M	TOT PER M	YOY PER M2
1995	EMR	1	4	0	0.166667	0.166667	0
1995	EMR	2	4	0	0.133333	0.133333	0
1995	EMR	3	5	0	0.208333	0.208333	0
1995	EMR	4	2	0	0.076923	0.076923	0
1995	EMR	5	12	0	0.444444	0.444444	0
1995	EMR	6	11	0	0.423077	0.423077	0
1995	EMR	7	10	0	0.5	0.5	0
1995	FC	1	7	0	0.212121	0.212121	0
1995	FC	2	17	0	0.586207	0.586207	0
1995	FC	3	18	0	0.642857	0.642857	0
1995	FC	4	42	0.333333	1.416667	1.75	0.200803
1995	FC	5	24	0	1	1	0
1995	FC	6	19	0.035714	0.642857	0.678571	0.023386
1995	FC	7	42	0.407407	1.148148	1.555556	0.261545
1995	FNC	1	0	0	0	0	0
1995	FNC	2	0	0	0	0	0
1995	FNC	3	16	0.04	0.6	0.64	0.015509
1995	FNC	4	0	0	0	0	0
1995	FNC	5	0	0	0	0	0
1995	FNC	6	0	0	0	0	0
1995	FNC	7	0	0	0	0	0
1995	GC	1	8	0.12	0.2	0.32	0.069398
1995	GC	2	7	0.12	0.16	0.28	0.083141
1995	GC	3	26	0.193548	0.645161	0.83871	0.108735
1995	GC	4	12	0.136364	0.409091	0.545455	0.086306
1995	GC	5	14	0.125	0.458333	0.583333	0.088548
1995	GC	6	0	0	0	0	0
1995	GC	7	8	0.086957	0.26087	0.347826	0.050343
1995	MRBC	1	1	0	0.043478	0.043478	0
1995	MRBC	2	3	0	0.12	0.12	0
1995	MRBC	3	4	0	0.137931	0.137931	0
1995	MRBC	4	4	0	0.148148	0.148148	0
1995	MRBC	5	4	0	0.133333	0.133333	0
1995	MRBC	6	3	0	0.125	0.125	0
1995	MRBC	7	8	0	0.307692	0.307692	0
1995	WMR	1	2	0	0.086957	0.086957	0
1995	WMR	2	0	0	0	0	0
1995	WMR	3	4	0	0.181818	0.181818	0
1995	WMR	4	3	0	0.130435	0.130435	0
1995	WMR	5	2	0	0.08	0.08	0
1995	WMR	6	2	0	0.074074	0.074074	0
1995	WMR	7	11	0	0.44	0.44	0
1995	T	1	0	0	0	0	0
1995	T	2	2	0	0.083333	0.083333	0
1995	T	3	3	0	0.09375	0.09375	0
1995	T	4	2	0	0.071429	0.071429	0
1995	T	5	14	0	0.411765	0.411765	0
1995	T	6	12	0	0.428571	0.428571	0
1995	T	7	3	0	0.142857	0.142857	0

Appendix 1. (cont.)

YEAR	STREAM	TRANSECT	ADU PER M2	TOT PER M2	YOY PER M3	ADU PER M3	TOT PER M3
1995	EMR	1	0.057962	0.057962	0	0.419461	0.419461
1995	EMR	2	0.049225	0.049225	0	0.438636	0.438636
1995	EMR	3	0.092627	0.092627	0	0.770108	0.770108
1995	EMR	4	0.019916	0.019916	0	0.203868	0.203868
1995	EMR	5	0.154156	0.154156	0	0.997031	0.997031
1995	EMR	6	0.186821	0.186821	0	1.298753	1.298753
1995	EMR	7	0.204082	0.204082	0	2.068395	2.068395
1995	FC	1	0.13341	0.13341	0	1.416739	1.416739
1995	FC	2	0.364265	0.364265	0	3.492955	3.492955
1995	FC	3	0.465839	0.465839	0	3.82881	3.82881
1995	FC	4	0.853414	1.054217	0.960015	4.080065	5.040081
1995	FC	5	0.633245	0.633245	0	5.252727	5.252727
1995	FC	6	0.420954	0.444341	0.153954	2.771172	2.925126
1995	FC	7	0.737083	0.998628	2.642558	7.447209	10.08977
1995	FNC	1	0	0	0	0	0
1995	FNC	2	0	0	0	0	0
1995	FNC	3	0.232633	0.248142	0.143159	2.147384	2.290543
1995	FNC	4	0	0	0	0	0
1995	FNC	5	0	0	0	0	0
1995	FNC	6	0	0	0	0	0
1995	FNC	7	0	0	0	0	0
1995	GC	1	0.115663	0.18506	0.71177	1.186284	1.898054
1995	GC	2	0.110855	0.193995	0.831409	1.108545	1.939954
1995	GC	3	0.36245	0.471185	0.867567	2.89189	3.759456
1995	GC	4	0.258918	0.345224	0.791139	2.373418	3.164557
1995	GC	5	0.324675	0.413223	1.066128	3.909134	4.975262
1995	GC	6	0	0	0	0	0
1995	GC	7	0.15103	0.201373	0.481544	1.444632	1.926176
1995	MRBC	1	0.015339	0.015339	0	0.10634	0.10634
1995	MRBC	2	0.045787	0.045787	0	0.25635	0.25635
1995	MRBC	3	0.046363	0.046363	0	0.319747	0.319747
1995	MRBC	4	0.048148	0.048148	0	0.35363	0.35363
1995	MRBC	5	0.049422	0.049422	0	0.456203	0.456203
1995	MRBC	6	0.049169	0.049169	0	0.625469	0.625469
1995	MRBC	7	0.109319	0.109319	0	0.775175	0.775175
1995	WMR	1	0.025796	0.025796	0	0.143796	0.143796
1995	WMR	2	0	0	0	0	0
1995	WMR	3	0.057094	0.057094	0	0.373089	0.373089
1995	WMR	4	0.03662	0.03662	0	0.268549	0.268549
1995	WMR	5	0.021267	0.021267	0	0.122303	0.122303
1995	WMR	6	0.024723	0.024723	0	0.177569	0.177569
1995	WMR	7	0.177122	0.177122	0	1.309319	1.309319
1995	T	1	0	0	0	0	0
1995	T	2	0.02425	0.02425	0	0.229302	0.229300
1995	T	3	0.028064	0.028064	0	0.273236	0.273236
1995	T	4	0.041118	0.041118	0	0.374615	0.374615
1995	T	5	0.172626	0.172626	0	1.482146	1.482146
1995	T	6	0.174763	0.174763	0	1.145502	1.145502
1995	T	7	0.0702	0.0702	0	0.735079	0.735079

Appendix 1. (cont.)

YEAR	STREAM	TRANSECT	AVG YOY MASS	AVG ADU MASS	TOT YOY MASS	TOT ADU MASS	TOTAL MASS
1995	EMR	1	0	13.15	0	52.6	52.6
1995	EMR	2	0	26.675	0	106.7	106.7
1995	EMR	3	0	25.7	0	128.5	128.5
1995	EMR	4	0	34.66667	0	69.33333	69.33333
1995	EMR	5	0	19	0	228	228
1995	EMR	6	0	11.35455	0	124.9	124.9
1995	EMR	7	0	12.33	0	123.3	123.3
1995	FC	1	0	37.18571	0	260.3	260.3
1995	FC	2	0	39.4625	0	670.8625	670.8625
1995	FC	3	0	30.21111	0	543.8	543.8
1995	FC	4	1.2125	36.64231	9.7	1245.839	1255.539
1995	FC	5	0	27.02609	0	648.6261	648.6261
1995	FC	6	1.4	36.3	1.4	653.4	654.8
1995	FC	7	1.71882	30.92903	18.90702	958.7999	977.707
1995	FNC	1	0	25.925	0	0	0
1995	FNC	2	0	16.74	0	0	0
1995	FNC	3	0.6	18.42143	0.6	276.3215	276.9215
1995	FNC	4	0	10.0375	0	0	0
1995	FNC	5	0	11.28	0	0	0
1995	FNC	6	0	18.42143	0	0	0
1995	FNC	7	0	9.285714	0	0	0
1995	GC	1	0.333333	39.64	1	198.2	199.2
1995	GC	2	0.4	32.55	1.2	130.2	131.4
1995	GC	3	0.516667	40.25	3.1	805	808.1
1995	GC	4	0.566667	38.28571	1.7	344.5714	346.2714
1995	GC	5	0.433333	25.5	1.3	280.5	281.8
1995	GC	6	0	24.25	0	0	0
1995	GC	7	0.5	24.46667	1	146.8	147.8
1995	MRBC	1	0	11.4	0	11.4	11.4
1995	MRBC	2	0	43.36667	0	130.1	130.1
1995	MRBC	3	0	26.625	0	106.5	106.5
1995	MRBC	4	0	23.85	0	95.4	95.4
1995	MRBC	5	0	11.575	0	46.3	46.3
1995	MRBC	6	0	14.83333	0	44.5	44.5
1995	MRBC	7	0	19.2	0	153.6	153.6
1995	WMR	1	0	25.7	0	51.4	51.4
1995	WMR	2	0	0	0	0	0
1995	WMR	3	0	60.875	0	243.5	243.5
1995	WMR	4	0	36.23333	0	108.7	108.7
1995	WMR	5	0	23.9	0	47.8	47.8
1995	WMR	6	0	88.25	0	176.5	176.5
1995	WMR	7	0	14.81818	0	163	163
1995	T	1	0	0	0	0	0
1995	T	2	0	57.85	0	115.7	115.7
1995	T	3	0	45.93333	0	137.8	137.8
1995	T	4	0	29.15	0	58.3	58.3
1995	T	5	0	15.625	0	218.75	218.75
1995	T	6	0	22.11667	0	265.4	265.4
1995	T	7	0	13.23333	0	39.7	39.7

Appendix 1. (cont.)

YEAR	STREAM	TRANSECT	GYOY PER M	GADU PER M	GTOT PER M	GYOY PER M2	GADU PER M2
1995	EMR	1	0	2.191667	2.191667	0	0.762198
1995	EMR	2	0	3.556667	3.556667	0	1.313069
1995	EMR	3	0	5.354167	5.354167	0	2.380511
1995	EMR	4	0	2.666667	2.666667	0	0.690434
1995	EMR	5	0	8.444444	8.444444	0	2.92897
1995	EMR	6	0	4.803846	4.803846	0	2.121264
1995	EMR	7	0	6.165	6.165	0	2.516327
1995	FC	1	0	7.887879	7.887879	0	4.96093
1995	FC	2	0	23.13319	23.13319	0	14.37482
1995	FC	3	0	19.42143	19.42143	0	14.0735
1995	FC	4	0.404167	51.90994	52.31411	0.243474	31.27105
1995	FC	5	0	27.02609	27.02609	0	17.11414
1995	FC	6	0.05	23.33571	23.38571	0.032741	15.28064
1995	FC	7	0.70026	35.51111	36.21137	0.44955	22.79725
1995	FNC	1	0	0	0	0	0
1995	FNC	2	0	0	0	0	0
1995	FNC	3	0.024	11.05286	11.07686	0.009305	4.285438
1995	FNC	4	0	0	0	0	0
1995	FNC	5	0	0	0	0	0
1995	FNC	6	0	0	0	0	0
1995	FNC	7	0	0	0	0	0
1995	GC	1	0.04	7.928	7.968	0.023133	4.584867
1995	GC	2	0.048	5.208	5.256	0.033256	3.608314
1995	GC	3	0.1	25.96774	26.06774	0.05618	14.58862
1995	GC	4	0.077273	15.66234	15.73961	0.048907	9.912871
1995	GC	5	0.054167	11.6875	11.74167	0.038371	8.279221
1995	GC	6	0	0	0	0	0
1995	GC	7	0.043478	6.382609	6.426087	0.025172	3.695195
1995	MRBC	1	0	0.495652	0.495652	0	0.174861
1995	MRBC	2	0	5.204	5.204	0	1.985628
1995	MRBC	3	0	3.672414	3.672414	0	1.234425
1995	MRBC	4	0	3.533333	3.533333	0	1.148333
1995	MRBC	5	0	1.543333	1.543333	0	0.572059
1995	MRBC	6	0	1.854167	1.854167	0	0.729338
1995	MRBC	7	0	5.907692	5.907692	0	2.098934
1995	WMR	1	0	2.234783	2.234783	0	0.662961
1995	WMR	2	0	0	0	0	0
1995	WMR	3	0	11.06818	11.06818	0	3.475592
1995	WMR	4	0	4.726087	4.726087	0	1.326875
1995	WMR	5	0	1.912	1.912	0	0.508285
1995	WMR	6	0	6.537037	6.537037	0	2.18181
1995	WMR	7	0	6.52	6.52	0	2.624623
1995	T	1	0	0	0	0	0
1995	T	2	0	4.820833	4.820833	0	1.402888
1995	T	3	0	4.30625	4.30625	0	1.289055
1995	T	4	0	2.082143	2.082143	0	1.198602
1995	T	5	0	6.433824	6.433824	0	2.697287
1995	T	6	0	9.478571	9.478571	0	3.865164
1995	T	7	0	1.890476	1.890476	0	0.928981

Appendix 1. (cont.)

YEAR	STREAM	TRANSECT	GTOT PER M2	GYOY PER M3	GADU PER M3	GTOT PER M3
1995	EMR	1	0.762198	0	5.515909	5.515909
1995	EMR	2	1.313069	0	11.70062	11.70062
1995	EMR	3	2.380511	0	19.79178	19.79178
1995	EMR	4	0.690434	0	7.06743	7.06743
1995	EMR	5	2.92897	0	18.94358	18.94358
1995	EMR	6	2.121264	0	14.74675	14.74675
1995	EMR	7	2.516327	0	25.50331	25.50331
1995	FC	1	4.96093	0	52.68244	52.68244
1995	FC	2	14.37482	0	137.8407	137.8407
1995	FC	3	14.0735	0	115.6726	115.6726
1995	FC	4	31.51452	1.164019	149.503	150.667
1995	FC	5	17.11414	0	141.9606	141.9606
1995	FC	6	15.31338	0.215536	100.5935	100.8091
1995	FC	7	23.2468	4.542082	230.335	234.877
1995	FNC	1	0	0	0	0
1995	FNC	2	0	0	0	0
1995	FNC	3	4.294743	0.085895	39.55789	39.64378
1995	FNC	4	0	0	0	0
1995	FNC	5	0	0	0	0
1995	FNC	6	0	0	0	0
1995	FNC	7	0	0	0	0
1995	GC	1	4.608	0.237257	47.02428	47.26154
1995	GC	2	3.64157	0.332564	36.08314	36.4157
1995	GC	3	14.6448	0.448243	116.3986	116.8468
1995	GC	4	9.961778	0.448312	90.86798	91.31629
1995	GC	5	8.317591	0.461989	99.68293	100.1449
1995	GC	6	0	0	0	0
1995	GC	7	3.720366	0.240772	35.34534	35.58611
1995	MRBC	1	0.174861	0	1.212273	1.212273
1995	MRBC	2	1.985628	0	11.11705	11.11705
1995	MRBC	3	1.234425	0	8.513275	8.513275
1995	MRBC	4	1.148333	0	8.434087	8.434087
1995	MRBC	5	0.572059	0	5.280544	5.280544
1995	MRBC	6	0.729338	0	9.277795	9.277795
1995	MRBC	7	2.098934	0	14.88335	14.88335
1995	WMR	1	0.662961	0	3.695562	3.695562
1995	WMR	2	0	0	0	0
1995	WMR	3	3.475592	0	22.71179	22.71179
1995	WMR	4	1.326875	0	9.730416	9.730416
1995	WMR	5	0.508285	0	2.923047	2.923047
1995	WMR	6	2.18181	0	15.67046	15.67046
1995	WMR	7	2.624623	0	19.40173	19.40173
1995	T	1	0	0	0	0
1995	T	2	1.402888	0	13.26513	13.26513
1995	T	3	1.289055	0	12.55064	12.55064
1995	T	4	1.198602	0	10.92002	10.92002
1995	T	5	2.697287	0	23.15853	23.15853
1995	T	6	3.865164	0	25.33469	25.33469
1995	T	7	0.928981	0	9.727549	9.727549

Appendix 2. Habitat data collected during 1994-5 surveys of Lahontan cutthroat trout streams. Column headings are defined as follows:

STR	Stream abbreviation.
SITE	Site number (="TRANSECT") in Appendix 1.
ZAVG	Mean stream depth (cm).
ZMAX	Maximum depth (cm).
WIDTH	Wetted stream width (cm).
UCUT	Undercut bank volume (m^3).
CAND	Canopy density (% points).
MACRO	Instream macrophyte cover (% points).
WOOD	Instream woody cover (% points).
CON	Conductivity (μS X 10).
PH	pH.
LWD	Number of large woody debris pieces.

Appendix 2. (cont.)

YEAR	STR	SITE	ZAVG	ZMAX	WIDTH	UCUT	CAND	MACRO	WOOD	CON	PH	LWD
1994	EMR	1	5.488	25	245.9	0	0.779	0	0	7	8.3	11
1994	EMR	2	6.76	19	222.7	0	0.068	0	0	7	8.4	0
1994	EMR	3	8.474	35	185.1	0	0.248	0	0	8	8.6	1
1994	EMR	4	5.622	19	173.9	0	0.097	0	0	7	8	1
1994	EMR	5	10.37	31	228.8	0.007	0.347	0	0.024	6	8.2	6
1994	EMR	6	9.417	29	171.5	0	0.718	0	0	6	8.6	6
1994	EMR	7	6.621	22	210.5	0	0.723	0	0.03	5	8.7	4
1994	FNC	1	9.167	26	230.3	0.004	0.845	0.128	0	7	8.5	6
1994	FNC	2	9.256	25	213.3	0.006	0.921	0	0.089	7	7.9	3
1994	FNC	3	9.893	30	199.8	0.005	0.838	0	0.214	7	7.4	5
1994	FNC	4	6.976	20	211.3	0	0.332	0.071	0.071	7	7.4	4
1994	FNC	5	12.21	30	251.7	0.003	0.794	0	0.02	7	8	4
1994	FNC	6	10.13	25	245.4	0.015	0.884	0	0.024	5	7.9	5
1994	FNC	7	10.77	32	226	0.001	0.706	0	0	7	8	11
1994	FR	2	10.56	36	119.7	0.000	0.718	0.154	0.077	16	7.8	0
1994	FR	3	9.318	29	111	0.001	0.605	0.051	0.077	17	7.8	5
1994	FR	4	16.79	71	163.3	0.013	0.681	0.095	0.214	15	7.6	2
1994	FR	5	9.208	41	145.7	0.001	0.6	0	0	15	7.8	1
1994	FR	6	10.18	60	126.4	0.005	0.933	0	0.154	14	8.1	4
1994	FR	7	7.544	21	177.5	0	0.472	0.689	0	14	8	7
1994	GC	1	8.298	21	166.2	0.002	0.519	0	0.048	29	8.1	3
1994	GC	2	7.94	15	150.2	0	0.58	0	0.143	27	7.8	0
1994	GC	3	9.222	27	156.7	0.003	0.454	0.089	0.311	29	8.1	3
1994	GC	4	7.818	19	151.8	0.001	0.083	0.061	0.061	33	8.3	0
1994	GC	5	8.487	27	188.7	0	0.62	0.333	0.077	28	8.4	4
1994	GC	6	10.64	28	129.1	0.002	0.697	0.333	0.205	36	8.1	1
1994	GC	7	9.269	26	159.5	0.001	0.368	0.385	0.026	35	8.3	1
1994	MRBC	1	9.369	30	183.1	0.002	0.83	0	0.024	6	8.2	5
1994	MRBC	2	10.71	41	206.6	0.001	0.813	0	0	6	8.5	4
1994	MRBC	3	8.538	25	167.3	0	0.618	0	0.077	6	8.7	10
1994	MRBC	4	6.548	24	193.4	0.002	0.954	0	0	7	8.6	1
1994	MRBC	5	8.644	27	211.6	0	0.597	0	0	10	8.7	7
1994	MRBC	6	4.022	20	160.1	0	0.807	0	0	11	8.8	9
1994	T	2	6.689	19	140.6	0.001	0.77	0	0.289	25	6.8	9
1994	T	3	6.071	20	169.9	0	0.853	0	0.071	25	7	7
1994	T	4	7.298	27	132.4	0.002	0.544	0	0.071	27	6.2	11
1994	T	5	8.989	39	180.4	0.002	0.785	0	0.133	26	6.8	15
1994	T	6	7.929	24	156	0	0.574	0	0	26	6.6	0
1994	T	7	5.545	15	137.8	0	0.946	0	0.03	23	6.5	5
1994	WMR	1	11.45	35	355.6	0	0.929	0	0.026	2	9.3	14
1994	WMR	2	12.58	31	218.6	0	0.412	0	0.061	2	9.6	8
1994	WMR	4	8.923	31	376.9	0	0.748	0	0	2	9	1
1994	WMR	5	12.79	29	320.4	0	0.151	0	0.024	2	9.3	15
1994	WMR	6	9.589	31	273.1	0	0.783	0	0.022	2	9.2	6
1994	WMR	7	7.641	25	301.5	0	0.739	0	0.026	2	9.2	13

Appendix 2. (cont.)

YEAR	STR	SITE	ZAVG	ZMAX	WIDTH	UCUT	CAND	MACRO	WOOD	CON	PH	LWD
1995	EMR	1	13.82	35	287.5	0	0.936	0	0	6	6.6	0
1995	EMR	2	11.22	29	270.9	0.000	0.127	0	0	6	6.7	0
1995	EMR	3	12.03	43	224.9	0	0.319	0	0	6	7.3	1
1995	EMR	4	9.769	17	386.2	0	0.087	0	0	6	7.1	0
1995	EMR	5	15.46	41	288.3	0.009	0.3	0	0.051	5	7.4	6
1995	EMR	6	14.38	41	226.5	0	0.63	0	0	6	7.3	1
1995	EMR	7	9.867	28	245	0	0.732	0	0	6	7.3	3
1995	FNC	1	12.17	42	229.3	0.002	0.489	0	0.026	10	7.7	4
1995	FNC	2	12.24	34	229.3	0.003	0.936	0	0.067	6	7.9	9
1995	FNC	3	10.83	43	257.9	0.012	0.855	0	0	6	8.3	5
1995	FNC	4	8.69	19	258.2	0	0.326	0	0.048	6	8.2	3
1995	FNC	5	12.49	38	222.9	0.003	0.768	0	0.022	5	7.9	3
1995	FNC	6	12.28	29	247.3	0.006	0.934	0	0	7	7.8	4
1995	FNC	7	9.444	30	246.3	0	0.691	0	0.056	7	8	10
1995	FR	2	10.43	36	160.9	0.001	0.71	0.214	0.024	17	7	1
1995	FR	3	12.17	32	138	0.002	0.548	0.119	0.071	14	7.2	0
1995	FR	4	20.92	44	166	0.012	0.784	0	0.333	14	6.7	1
1995	FR	5	12.06	40	157.9	0.000	0.478	0.389	0	14	7.3	4
1995	FR	6	15.19	46	152.7	0.004	0.958	0	0	10	7.3	1
1995	FR	7	9.897	30	155.8	0	0.328	0.59	0	14	7.2	5
1995	GC	1	9.75	25	172.9	0	0.466	0	0	34	7.2	0
1995	GC	2	10	19	144.3	0	0.547	0.111	0.028	34	7.3	0
1995	GC	3	12.53	44	178	0.001	0.504	0	0	33	7.3	5
1995	GC	4	10.91	34	158	0.002	0.186	0	0	27	7.4	0
1995	GC	5	8.306	24	141.2	0	0.642	0	0.056	33	6.4	0
1995	GC	6	11.08	35	136.9	0.000	0.563	0.128	0.026	36	6.8	0
1995	GC	7	10.45	29	172.7	0.000	0.397	0	0	25	7.3	1
1995	MRBC	1	14.42	42	283.5	0.001	0.843	0	0	6	7	2
1995	MRBC	2	17.86	48	262.1	0.001	0.924	0	0.056	6	6.6	4
1995	MRBC	3	14.5	41	297.5	0.001	0.611	0	0	8	5.7	5
1995	MRBC	4	13.62	38	307.7	0.000	0.926	0	0	10	7.7	4
1995	MRBC	5	10.83	37	269.8	0.006	0.716	0	0	12	6.7	6
1995	MRBC	6	7.861	20	254.2	0	0.742	0	0	9	7.5	5
1995	T	2	10.58	25	343.6	0.000	0.603	0	0.091	13	7	12
1995	T	3	10.27	30	334.1	0.001	0.827	0	0	13	7.2	4
1995	T	4	10.98	25	173.7	0.004	0.534	0	0.024	16	7.2	8
1995	T	5	11.65	55	238.5	0.001	0.68	0	0.176	15	7.1	18
1995	T	6	15.26	55	245.2	0.001	0.622	0	0	13	7	0
1995	T	7	9.55	20	203.5	0	0.735	0	0.033	11	6.4	4
1995	WMR	1	17.94	37	337.1	0	0.917	0	0	2	5.8	7
1995	WMR	2	21.76	65	269.3	0	0.407	0	0	2	7.5	1
1995	WMR	4	13.64	33	356.2	0.001	0.74	0	0	2	7.4	5
1995	WMR	5	17.39	52	376.2	0.017	0.297	0	0	2	7.5	7
1995	WMR	6	13.92	42	299.6	0.009	0.861	0	0	2	7.3	7
1995	WMR	7	13.53	43	248.4	0.002	0.843	0	0	3	7.4	16

Appendix 3. Variables used in incidence-function analysis (see Chapter 2).

Number	Stream Name	Latitude	Longitude	Presence or Absence Fragmentation	LCT
2	ABEL CREEK	41.43099	117.7008	0	1
3	ACKLER CREEK	41.00366	115.2067	0	0
4	ALLES CREEK	41.00366	115.2067	0	0
5	ALTA CREEK	41.78011	118.629	0	0
6	ANDORNO CREEK	41.43099	117.7008	0	0
7	AUSTIN CREEK	41.43099	117.8168	0	0
8	BATTLE CREEK	41.18476	118.7931	0	0
9	BEADLES CREEK	41.53632	116.0142	1	0
10	BEAVER CREEK, EF	41.61858	115.6614	0	0
11	BEAVER CREEK, WF	41.61858	115.6614	0	0
12	BOONE CREEK	39.77425	117.2565	0	0
13	BOTTLE CREEK	41.34346	118.2816	0	1
14	BUFFALO CANYON CRE	41.43099	117.7008	0	1
15	BUTTERFIELD CREEK	40.65448	115.5548	0	0
16	CABIN CREEK	41.69283	117.5848	1	1
17	CHIMNEY CREEK	41.70585	115.4284	1	1
18	CHIMNEY CREEK	41.43099	117.7008	0	0
19	CLEAR CREEK	38.99256	117.3746	0	0
20	CLEARWATER CANYON	40.73486	117.7084	0	0
21	COLD SPRINGS CREEK	41.95467	118.2809	1	1
22	COLE CANYON CREEK	41.62309	116.0142	1	1
23	CONRAD CREEK	40.65448	115.3253	0	1
24	COTTONWOOD CREEK	41.51827	117.5848	0	1
25	COTTONWOOD CREEK	40.47997	115.6703	0	1
26	COTTONWOOD CREEK	39.16196	117.2643	0	1
27	CROWLEY CREEK	41.78011	117.9328	0	1
28	CUTT CREEK	41.53132	115.4284	1	1
29	DEERING CREEK	41.00366	115.2067	0	0
31	DELL CREEK	41.53632	115.8973	0	0
32	DIXIE CREEK	40.47997	115.8981	0	1
33	DRAW CREEK	41.70585	115.3119	1	1
35	EAST FORK BOULDER	41.00366	115.2067	1	1
36	EAST FORK QUINN RI	41.95467	117.7008	1	1
37	EIGHTMILE CREEK	41.86739	117.5848	0	1
38	FISH CREEK	40.20972	117.3702	0	0
39	FOREMAN CREEK	41.36197	115.7846	0	1
40	FRAZER CREEK	41.25948	116.6743	0	1
41	GAWS CREEK	41.53132	115.4284	1	1
42	GENETTEE CREEK	40.47997	115.5564	1	1
43	HALL CREEK	41.09121	115.2067	0	0
44	HERDER CREEK	41.00366	115.2067	0	0
45	HOT SPRINGS CREEK	41.18561	115.9004	0	0
46	IOWA CREEK	39.77425	117.0311	0	0
47	ITALIAN CREEK	39.59926	117.0346	0	0
48	JACKSON CREEK	41.34346	118.6265	0	0
49	JAKES CREEK	41.95467	117.5848	0	0
50	KELLEY CREEK	41.25948	117.0193	0	0
51	KINGS RIVER	41.51827	118.1649	1	1
52	KLECKNER CREEK	40.5672	115.5548	1	0

Number	Stream Name	Latitude	Longitude	Presence or Absence Fragmentation	LCT
53	LAMOILLE CREEK	40.65448	115.44	0	0
54	LEE CREEK	40.65448	115.5548	0	1
55	LEWIS CREEK	41.25948	116.4444	1	1
55.5	SF LITTLE HUMB	41.347	116.9043	1	1
56	LITTLE JACK CREEK	41.00925	116.2476	1	1
57	LONG CANYON CREEK	41.95467	117.4688	1	1
58	LONG CANYON CREEK	40.5672	115.5548	1	1
60	LOST CREEK	41.00366	115.2067	0	0
62	LYE CREEK	41.69283	117.5848	1	1
63	MAGGIE CREEK	40.74644	116.2381	1	1
64	MAHOGANY CREEK	41.55637	119.0147	1	1
65	MAHOGANY CREEK	40.5672	115.44	1	1
66	MARY SLOAN CREEK	41.34346	118.5115	0	1
67	MARYS RIVER BASIN	41.70585	115.4284	1	1
68	MARYSVILLE CREEK	39.07835	117.3746	0	1
69	MCAFEE CREEK	41.53632	116.0142	0	0
70	MCDERMITT CREEK	42.04195	117.8168	1	1
71	MITCHELL CREEK	40.21795	115.6703	0	1
72	MOREY CREEK	41.43099	117.5848	0	0
73	MULLINIX CREEK	41.60555	117.5848	0	0
74	NELSON CREEK	41.25948	116.4444	1	1
75	NORTH FORK HUMBOLD	41.00925	115.9004	1	1
76	NORTH FORK LITTLE	41.78011	117.3527	1	1
77	NORTH FURLONG	40.5672	115.44	1	1
78	PAIUTE CREEK	41.37244	119.0173	0	0
79	PETERMAN CREEK	41.43099	117.8168	0	0
80	PETERSON CREEK	40.65448	115.5548	0	0
81	PETERSON CREEK	41.53632	115.8973	1	0
82	PIE CREEK	41.27379	115.7846	0	0
83	PINE CREEK	40.13518	116.4532	0	0
84	PORCUPINE CREEK	41.43099	117.7008	0	0
85	PRATT CREEK	41.44405	115.5449	0	0
86	PROVO CANYON CREEK	41.43099	117.7008	0	0
87	RATTLESNAKE CREEK	40.47997	115.5564	1	1
89	REBEL CREEK	41.60555	117.7008	0	1
90	RISER CREEK	41.95467	118.0489	0	1
91	ROCK CREEK	41.347	116.4444	0	1
92	SAMMY CREEK	41.53632	116.0142	1	0
93	SECRET CREEK	41.25948	116.9043	1	1
94	SEGUNDA CREEK	40.5672	115.44	1	1
95	SHEEP CREEK	41.347	116.9043	1	1
96	SHORT CREEK	41.70585	115.4284	1	1
97	SMILEY CREEK	41.00366	115.2067	0	0
98	SMITH CREEK	40.39263	115.6703	1	1
99	SOLDIER CREEK	40.74176	115.3253	0	0
100	SONOMA CREEK	40.73486	117.8225	0	0
101	SOUTH FORK QUINN R	41.95467	117.4688	1	0
102	STONEHOUSE CREEK	41.43099	117.7008	1	0
103	SUSIE CREEK	40.92155	116.0134	0	0
104	T CREEK	41.53132	115.3119	1	1
105	THOMAS CREEK	40.90893	117.5944	0	0

Number	Stream Name	Latitude	Longitude	Presence or Absence Fragmentation	LCT
106	THREEMILE CREEK	41.86739	117.7008	0	1
107	TIERNEY CREEK	39.16414	117.3746	0	1
108	TOE JAM CREEK	41.34346	117.4767	1	1
109	TROUT CREEK	41.09121	115.0912	0	0
110	TROUT CREEK	41.25655	118.5115	0	0
111	TROUT CREEK	40.38515	116.9177	0	0
112	UPPER HUNTINGTON C	40.04529	115.784	0	0
113	UPPER MARYS RIVER	41.70585	115.4284	1	1
114	UPPER REESE RIVER	38.82097	117.3746	0	0
115	UPPER SOUTH FORK H	40.5672	115.5548	1	1
116	WALKER CREEK	41.53632	115.8973	0	0
118	WASH O'NEAL CREEK	41.43099	117.7008	0	0
119	WASHBURN CREEK	41.95467	117.9328	0	1
120	WELCH CREEK	40.65448	115.5548	1	1
121	WEST FORK BOULDER	40.91633	115.2105	1	1
122	WEST MARYS RIVER	41.53132	115.4284	1	1
123	WILLIAMS BASIN CRE	41.53132	115.4284	1	1
124	WILLOW CREEK	40.47997	115.6703	0	0
125	WILLOW CREEK	41.25948	116.5594	1	1

Number	<--Presence or Absence--> Brook trout	Rainbow trout	Brown trout	Basin area	Basin length (km)	Relief ratio	Elongation ratio
2	1	0	0	25.14326	7.7066	2.363821	18.85786
3	1	0	0	94.20161	14.33442	4.773924	8.516826
4	0	0	0	7.2584	7.27518	1.125368	21.72753
5	1	0	0	17.06712	7.59862	1.898283	15.93376
6	0	0	0	10.50484	6.48913	1.421837	28.35511
7	0	0	0	2.67006	3.27834	0.553785	88.39254
8	0	0	0	54.7512	10.42155	3.597919	9.124499
9	0	0	0	3.26865	3.61747	0.645507	67.24698
10	0	0	0	139.239	20.41342	5.834525	1.375065
11	0	0	0	306.0393	29.56607	8.702436	0.655492
12	1	0	0	42.66402	15.13803	3.1519	5.345611
13	0	1	0	29.77692	7.89741	2.594954	18.21415
14	0	0	0	18.76606	7.46831	2.004681	24.56269
15	0	0	0	16.41684	17.37326	1.856062	5.632307
16	1	1	1	25.08672	8.85215	2.360866	7.899382
17	0	0	0	16.73377	8.38214	1.876749	12.38253
18	0	0	0	10.0068	6.56449	1.379841	25.52647
19	1	0	0	32.09947	15.23925	2.703606	5.274835
20	1	1	0	87.01257	13.23032	4.582042	7.141169
21	0	1	0	11.65047	5.16043	1.514604	22.53095
22	0	0	0	10.2812	4.00324	1.403112	34.94337
23	1	0	0	9.16185	8.81255	1.30599	17.38323
24	1	1	0	28.45281	7.63846	2.530988	31.55311
25	0	0	0	16.84973	8.49524	1.884266	19.05247
26	1	1	1	22.58172	8.83169	2.226197	10.98736
27	0	0	0	47.05344	12.53088	3.32071	4.126785
28	0	0	0	21.65812	5.566	2.17454	34.53801
29	0	0	0	11.54361	6.601	1.506162	10.05205
31	0	0	0	5.35246	6.10117	0.918261	22.56592
32	0	0	0	101.5805	15.58618	4.963194	3.852978
33	0	0	0	11.3157	7.3062	1.488017	12.92605
35	1	0	0	28.54398	13.3298	2.535442	8.723373
36	1	1	1	256.0715	23.12828	7.952484	1.486211
37	0	0	0	44.14991	10.48523	3.210024	9.095866
38	0	0	0	173.7216	20.35777	6.531382	1.918257
39	0	0	0	20.6403	9.02026	2.11623	13.86344
40	0	0	0	27.0671	10.92485	2.462327	6.283915
41	0	0	0	7.71518	3.74367	1.170754	39.31484
42	1	0	0	13.84707	7.35926	1.679764	23.00646
43	1	0	0	3.48229	4.34262	0.676517	57.79933
44	1	0	0	23.41412	13.53879	2.271794	8.865305
45	0	0	0	6.46493	8.48909	1.042919	9.019679
46	0	1	0	97.95896	21.7662	4.871216	2.374583
47	0	0	0	57.53808	16.4203	3.693208	4.357884
48	1	0	0	36.66806	7.14304	2.905787	22.26446
49	1	1	0	26.36835	9.39247	2.426994	9.635168
50	1	1	0	128.7777	17.40201	5.606045	3.503616
51	0	1	0	38.38383	9.82763	2.978251	10.87156
52	1	0	0	21.89353	13.14732	2.187817	8.388678
53	1	1	0	161.9783	25.62487	6.302707	2.709272
54	0	0	0	12.90229	12.20346	1.610579	10.7437

Number	<--Presence or Absence--> Brook trout	Rainbow trout	Brown trout	Basin area	Basin length (km)	Relief ratio	Elongation ratio
55	0	0	0	30.20914	9.58413	2.615506	9.700013
55.5	0	0	0	66.71063	9.66328	3.990938	7.014427
56	0	0	0	29.56305	17.15775	2.584726	2.95528
57	0	0	0	8.92271	6.19083	1.284445	12.39355
58	0	0	1	103.2063	8.50794	5.003936	20.72251
60	0	0	0	3.28226	4.42986	0.647508	45.86301
62	0	1	0	7.66601	6.26698	1.165936	25.23231
63	0	0	0	644.428	23.0747	12.66197	1.880018
64	0	0	0	11.01129	11.35481	1.463476	5.483523
65	1	0	0	15.51626	6.37522	1.796082	22.63588
66	0	1	0	9.80586	5.07667	1.362585	38.80093
67	0	0	0	18.95674	6.41646	2.016294	19.6012
68	1	0	0	38.70097	14.89644	2.991457	5.231994
69	0	0	0	27.81647	9.95749	2.499684	12.62713
70	1	1	1	425.3517	20.65087	10.27416	2.344894
71	0	0	0	56.32576	16.81396	3.652059	5.302267
72	0	0	0	9.20741	7.55583	1.310061	23.99696
73	0	1	0	41.76896	10.34202	3.116373	10.82674
74	0	0	0	70.00833	11.35625	4.092727	4.846298
75	1	0	0	115.9272	15.56348	5.31198	5.168814
76	1	1	1	181.6308	16.77851	6.680991	3.037102
77	0	0	0	16.30574	11.24342	1.84876	11.23289
78	0	0	0	69.32039	10.78691	4.071701	7.305077
79	0	0	0	3.43671	4.8425	0.669971	44.77649
80	0	0	0	6.05513	4.92975	0.998336	36.00462
81	1	0	0	12.21008	7.51106	1.558155	18.78899
82	0	0	0	40.21795	13.83133	3.053849	2.927252
83	0	0	0	555.4756	35.51251	11.75108	0.884122
84	0	0	0	7.18133	6.06657	1.117567	30.97551
85	1	0	0	29.43944	13.71698	2.578797	6.866659
86	0	1	0	17.14024	7.00521	1.902976	23.23071
87	1	0	0	25.74173	15.68941	2.394882	6.548651
89	1	1	0	27.18655	7.02648	2.468318	29.511
90	1	1	0	77.41028	10.17621	4.312517	6.498946
91	0	0	0	501.4631	21.25362	11.16178	2.10309
92	0	0	0	2.20449	3.23122	0.476717	76.62261
93	0	0	0	18.11136	5.77962	1.964316	17.2135
94	1	0	0	14.3149	7.03483	1.713089	25.25822
95	0	0	0	37.41066	7.11925	2.937365	11.83812
96	0	0	0	3.83278	11.48268	0.725657	3.337076
97	0	0	0	5.11303	5.68596	0.889815	28.76573
98	1	0	1	60.21831	17.61226	3.782608	5.367648
99	1	0	0	72.93012	13.11818	4.180857	8.449232
100	1	1	0	35.7525	9.32289	2.866385	15.69326
101	0	1	1	60.54993	12.71876	3.793524	4.91448
102	1	0	0	8.20554	6.13686	1.217963	27.88026
103	0	0	0	484.8755	28.9903	10.97445	1.261248
104	0	0	0	26.04072	9.72037	2.410256	9.313589
105	0	1	0	21.76784	8.35452	2.180738	18.62517
106	0	0	0	22.59383	8.1134	2.226867	17.69784

Number	<--Presence or Absence--> Brook trout	Rainbow trout	Brown trout	Basin area	Basin length (km)	Relief ratio	Elongation ratio
107	1	0	0	47.34601	16.8727	3.331663	3.593407
108	0	0	0	65.13758	19.1602	3.941463	2.495143
109	1	0	0	34.79579	12.5686	2.824639	8.989065
110	0	0	0	27.74985	10.10856	2.496385	7.339774
111	1	1	0	35.77718	15.30643	2.867455	5.723754
112	0	1	1	1721.008	67.9875	20.72361	0.369946
113	0	0	0	75.93111	8.70012	4.269495	14.79679
114	1	1	1	258.0643	22.16225	7.983741	3.182228
115	0	0	0	220.897	18.54551	7.379015	4.686919
116	0	0	0	11.74725	6.76503	1.522214	21.85046
118	1	1	0	17.29865	9.62471	1.913107	11.87456
119	0	0	0	33.28488	23.32556	2.757455	1.194673
120	0	0	0	6.25028	6.26099	1.019749	36.9898
121	1	0	0	28.08039	13.36595	2.512713	8.67625
122	0	0	0	31.96965	7.21445	2.697645	21.13422
123	0	0	0	6.49364	3.91015	1.045989	51.67021
124	0	0	0	15.42067	13.23595	1.789607	7.825773
125	0	0	0	317.3089	15.53698	8.862817	2.464812

Number	Basin shape factor	Maximum elevation	Minimum elevation	Mean elevation	6 hour, 100 year precipitation (cm)
2	2.362131	2670	1550	2110	16
3	2.181232	3400	1650	2525	23
4	7.291999	2950	1800	2375	23
5	3.383056	2420	1500	1960	18
6	4.008515	2694	1500	2097	16
7	4.025195	2450	1500	1975	16
8	1.983677	2491	1500	1995.5	18
9	4.003515	3000	2120	2560	21
10	2.992752	2313	1740	2026.5	19
11	2.856341	2313	1740	2026.5	19
12	5.37127	2850	1625	2237.5	21
13	2.094545	2636	1500	2068	18
14	2.972156	2870	1500	2185	16
15	18.3854	3350	1650	2500	23
16	3.123587	2444	1825	2134.5	18
17	4.198711	2750	1880	2315	22
18	4.306325	2600	1500	2050	16
19	7.234847	3250	2025	2637.5	24
20	2.011679	2750	1500	2125	18
21	2.285748	2550	1950	2250	18
22	1.558761	2680	2120	2400	19
23	8.476567	3200	1850	2525	23
24	2.050626	3341	1500	2420.5	18
25	4.283101	3150	1775	2462.5	23
26	3.454066	2957	2100	2528.5	22
27	3.33712	2148	1500	1824	16
28	1.430427	2950	1880	2415	21
29	3.77466	2238	1800	2019	23
31	6.954611	2800	1960	2380	21
32	2.391492	2666	1730	2198	19
33	4.717389	2640	1950	2295	22
35	6.224905	3300	1750	2525	23
36	2.088937	2295	1500	1897.5	18
37	2.490153	2500	1500	2000	16
38	2.385649	2295	1500	1897.5	21
39	3.94205	3108	1980	2544	21
40	4.409499	2350	1600	1975	18
41	1.816557	2911	2360	2635.5	23
42	3.911203	3196	1950	2573	23
43	5.415502	2880	1790	2335	23
44	7.82856	3275	1650	2462.5	23
45	11.14701	2480	1830	2155	20
46	4.836387	2800	1675	2237.5	21
47	4.686049	2850	1675	2262.5	21
48	1.391484	2636	1500	2068	18
49	3.345621	2350	1500	1925	20
50	2.351571	2561	1500	2030.5	20
51	2.516224	2550	1500	2025	18
52	7.895119	3300	1850	2575	23
53	4.053839	3449	1670	2559.5	23
54	11.54248	3350	1750	2550	23

Basin

Number	shape factor	Maximum elevation	Minimum elevation	Mean elevation	6 hour, 100 year precipitation (cm)
55	3.040654	2566	1675	2120.5	20
55.5	1.399762	2555	1900	2227.5	20
56	9.957984	2600	1730	2165	18
57	4.295374	2100	1625	1862.5	16
58	0.701363	3350	1850	2600	23
60	5.978704	2950	2050	2500	23
62	5.12327	2966	1975	2470.5	18
63	0.826224	2676	1675	2175.5	20
64	11.70905	2486	1779	2132.5	18
65	2.619409	3320	2400	2860	23
66	2.628283	2500	1500	2000	16
67	2.171838	2907	2100	2503.5	22
68	5.733808	3286	2125	2705.5	24
69	3.564493	3182	1930	2556	21
70	1.002602	2500	1500	2000	18
71	5.019182	3224	1725	2474.5	22
72	6.200502	2870	1500	2185	16
73	2.56069	2658	1500	2079	18
74	1.84213	2300	1675	1987.5	20
75	2.089431	3182	1930	2556	21
76	1.549949	2665	1810	2237.5	18
77	7.75276	3320	1900	2610	23
78	1.678545	2350	1500	1925	18
79	6.82333	2550	1500	2025	16
80	4.013528	2600	1725	2162.5	23
81	4.620447	3040	1980	2510	21
82	4.756724	2360	1800	2080	20
83	2.270376	2790	1675	2232.5	21
84	5.124855	2640	1500	2070	16
85	6.391274	3182	1890	2536	21
86	2.863027	2640	1500	2070	16
87	9.562589	3362	1750	2556	23
89	1.816024	2957	1500	2228.5	18
90	1.337745	2173	1500	1836.5	16
91	0.900797	2600	1650	2125	20
92	4.736144	3040	2240	2640	21
93	1.844368	2475	1900	2187.5	20
94	3.457155	3300	2050	2675	23
95	1.354794	2500	1900	2200	20
96	34.40112	2400	1960	2180	22
97	6.323088	2720	1790	2255	23
98	5.151119	3335	1670	2502.5	23
99	2.35961	3154	1700	2427	23
100	2.431055	2864	1500	2182	18
101	2.671627	2295	1500	1897.5	16
102	4.58971	2600	1550	2075	16
103	1.733306	2560	1500	2030	20
104	3.628379	2800	1920	2360	22
105	3.206474	2800	1500	2150	18
106	2.913506	2665	1500	2082.5	18
107	6.012925	3148	2125	2636.5	22

Number	Basin shape factor	Maximum elevation	Minimum elevation	Mean elevation	6 hour, 100 year precipitation (cm)
108	5.635967	2566	1650	2108	20
109	4.539909	3140	1720	2430	23
110	3.68229	2250	1500	1875	18
111	6.548498	2841	1500	2170.5	21
112	2.685809	3335	1625	2480	22
113	0.996852	3220	2100	2660	23
114	1.903267	3588	2025	2806.5	24
115	1.556997	3362	1750	2556	23
116	3.895859	2960	1960	2460	21
118	5.355045	2600	1500	2050	16
119	16.34621	2150	1500	1825	16
120	6.271718	3350	1900	2625	23
121	6.362042	3300	1750	2525	23
122	1.628053	3220	2120	2670	23
123	2.3545	2750	1960	2355	22
124	11.36075	3146	1775	2460.5	22
125	0.760766	2270	1675	1972.5	20

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